Volume XXIX. No. 4 October, 1954

THE JOURNAL OF HORTICULTURAL SCIENCE

(*Formerly The Journal of Pomology and Horticultural Science*)

Subscription Rates:
SINGLE NUMBERS 15/- EACH
ONE VOLUME (FOUR NUMBERS) 50/- (RATE FOR CANADA & U.S.A., $7.00) POST FREE

PUBLISHED BY
HEADLEY BROTHERS LTD
109 Kingsway London WC2 England

COMMONWEALTH MYCOLOGICAL
10 NOV 1954

THE JOURNAL OF HORTICULTURAL SCIENCE

The suggested abbreviation for the title of this publication is *J. hort. Sci.*

Back numbers of the JOURNAL, together with comprehensive Author and Subject Indexes to Volumes I to X and Volumes XI to XX, are available from the Publishers.

JOINT EDITORS

Prof. T. WALLACE, C.B.E., M.C., D.Sc., F.R.I.C., V.M.H., F.R.S., Horticultural Research Station, Long Ashton, Bristol.

T. N. HOBLYN, Hort. Dip., East Malling Research Station, near Maidstone, Kent.

ASSISTANT EDITOR

W. M. WARE, D.Sc., Brookfield, Wye, near Ashford, Kent.

PUBLICATION COMMITTEE

D. AKENHEAD, O.B.E., M.A., B.Sc., Commonwealth Bureau of Horticulture and Plantation Crops, East Malling Research Station, near Maidstone, Kent.

W. F. BEWLEY, C.B.E., D.Sc., V.M.H., Experimental and Research Station, Cheshunt, Herts.

Prof. W. BROWN, M.A., D.Sc., F.R.S., The Bush, Haddenham, Aylesbury, Bucks.

E. E. CHEESMAN, D.Sc., A.R.C.S., Agricultural Research Council, Cunard Building, 15 Regent Street, London, S.W.1.

M. B. CRANE, A.L.S., V.M.H., F.R.S., Firs Farm, Haughley, nr. Stowmarket, Suffolk.

Sir R. G. HATTON, C.B.E., M.A., D.Sc., V.M.H., F.R.S., 23 Hillside Street, Hythe, Kent.

C. E. HUDSON, N.D.H., V.M.H., Ministry of Agriculture and Fisheries, 1-4 Cambridge Terrace, Regent's Park, London, N.W.1.

F. KIDD, C.B.E., M.A., D.Sc., F.R.S., Low Temperature Research Station, Downing Street, Cambridge.

Prof. E. J. MASKELL, F.R.S., Botanical Department, The University, Edgbaston, Birmingham 15.

Prof. H. W. MILES, D.Sc., Ph.D., Wye College (University of London), near Ashford, Kent.

Prof. J. W. MUNRO, C.B.E., M.A., D.Sc., Frognal Cottage, Larch Avenue, Sunninghill, Berks.

T. NEAME, M.A., V.M.H., Macknade, Faversham, Kent.

J. PHILP, B.Sc., Ph.D., F.L.S., National Vegetable Research Station, Wellesbourne, Warwick.

Prof. R. H. STOUGHTON, D.Sc., The University, Reading, Berks.

F. R. TUBBS, M.Sc., Ph.D., East Malling Research Station, near Maidstone, Kent.

ASSOCIATE EDITORS

F. G. ANDERSSEN, B.Sc., Ph.D., Department of Agriculture, Division of Horticulture, P.O. Box 994, 590 Vermeulen Street, Pretoria, South Africa.

Prof. R. E. D. BAKER, M.A., A.I.C.T.A., Imperial College of Tropical Agriculture, Trinidad, B.W.I.

Prof. B. T. P. BARKER, C.B.E., M.A., c/o Horticultural Research Station, Long Ashton, Bristol.

C. BARNARD, D.Sc., Division of Plant Industry, Council of Scientific and Industrial Research, Canberra City, F.C.T., Australia.

Prof. V. H. BLACKMAN, Sc.D., F.R.S., 17 Berkeley Place, Wimbledon, London, S.W.19.

M. B. DAVIS, B.S.A., M.Sc., Central Experimental Farm, Ottawa, Canada.

K. S. DODDS, D.Sc., John Innes Horticultural Institute, Bayfordbury, Hertford, Herts.

W. C. MOORE, M.A., Ministry of Agriculture and Fisheries, Plant Pathology Laboratory, Milton Road, Harpenden, Herts.

Sir E. J. SALISBURY, C.B.E., D.Sc., L.L.D., F.L.S., V.M.H., V.P.R.S., Royal Botanic Gardens, Kew, Surrey.

Emeritus Prof. E. S. SALMON, F.L.S., Wye College, near Ashford, Kent.

H. V. TAYLOR, C.B.E., D.Sc., A.R.C.S., V.M.H., Preston Grange, Barnet Road, Potters Bar, Middlesex.

L. W. TILLER, B.Sc., Department of Scientific and Industrial Research, Wellington, C.1, New Zealand.

THE EFFECTS OF DEFICIENCIES AND EXCESSES OF SOME MINERAL NUTRIENTS ON THE GROWTH OF TULIP AND DAFFODIL BULBS IN SAND CULTURE

By E. J. HEWITT* and PEGGY MILES†
*Long Ashton Research Station, Bristol and †National Agricultural Advisory Service, Kirton Farm Institute, Boston, Lincs.

EARLY experiments on bulb nutrition were carried out by Handley (2) at Kirton Experimental Station and by Bould (1) and Stoughton (9) at Reading University. The Kirton experiment was on the tulip, variety Princess Elizabeth, and was restricted to the production of deficiencies of nitrogen, potassium and phosphorus, in addition to complete nutrient and rain water only treatments. Bould also studied the effects of deficiencies of N, P and K on tulip, variety Farncombe Sanders, and daffodil, variety King Alfred. Stoughton (9) studied the effects of factorial combinations of N, P and K on the growth of Dutch iris in sand culture.

The present experiments were begun at Long Ashton to study the effects of deficiencies of these elements and also of calcium and magnesium, and of excess of manganese, on the growth of the bulb and on visual symptoms produced in the plants.

The first experiment consisted of a preliminary trial with tulips only, to study the effect of initial bulb size on subsequent growth. The main experiment was made with tulip and daffodil bulbs graded for size and weight ; the bulbs were lifted and replanted annually and the respective treatments continued for a total period of three years.

EXPERIMENTAL.

METHODS.

Ten-inch unglazed clay pots with a central drainage hole were coated three times on the inner surface with bitumen paint to prevent contamination from the pot. The hole was covered with glass wool surmounted by a 2½-in. diameter watch-glass.

A quartz sand of 20–40 mesh grade was used for growth. It was first leached with cold 3 per cent. hydrochloric acid to remove easily soluble impurities, then with rain water to remove free acid, and finally with appropriate nutrient solutions until it was neutral.

Rain water, collected from the greenhouse roof, was stored in galvanized tanks, coated on the inside with bitumen paint. The water contained approximately 1 p.p.m. of calcium and potassium, and 0·1 p.p.m. of magnesium.

Nutrient solutions were prepared with rain water according to the formulae drawn up by Hewitt (7) using recrystallized grade salts. The concentrations of elements in the solutions as supplied were as follows, in p.p.m. :

N, 142 ; P, 41 ; S, 48 ; Ca, 160 ; Mg, 37 ; K, 78 ; Na, 30 ; Fe, 5·6 ; Mn, 0·55 ; Cu, 0·064 ; Zn, 0·065 ; B, 0·37 ; Mo, 0·019.

500 ml. of solution per pot was supplied as needed. Rain water alone was used about every sixth watering to avoid the accumulation of unused nutrients.

Plant material.

In the preliminary experiment, tulip bulbs, variety Rose Copland, of 5 and 12 cm. circumference were used, and 5 and 4 respectively were planted in each pot. For the main three-year experiment, tulip variety Rose Copland and daffodil variety King Alfred were used. In the first year, tulip bulbs of 7 cm. circumference weighing between 7·20 and 9·80 g., five per pot, and daffodil bulbs of 12 cm. or more, weighing between 21·5 and 29·0 g., four per pot, were planted. Tulip bulbs for replanting were drawn at random from the largest (main) bulbs produced in each treatment. The daffodil bulbs were given hot water treatment before the first planting, and representative large bulbs were chosen for replanting.

At the end of each year the harvested bulbs were sampled for analysis, the results of which are reported separately.

During the first year the pots were arranged in four blocks containing both varieties. The varieties were separated in the second and third years for ease of working. There were the following eight treatments, with two pots of each variety in each block : complete nutrient, high nitrogen, omitting nitrogen, omitting potassium, omitting phosphorus, omitting calcium, omitting magnesium, medium calcium plus high manganese. The high nitrogen treatment provided 284 p.p.m. N. The excess manganese treatment provided 55 p.p.m. Mn with a medium Ca level of 133 p.p.m. This was included to test the effects of one of the soil acidity factors studied by Hewitt (6) in a range of crops.

The bulbs were weighed separately before being placed in a marked position in the pot. At the end of the growing season they were reweighed, labelled and stored throughout the summer. In the following autumn they were weighed again, replanted into fresh sand in the same pots and the respective treatments continued. Owing to the removal of samples for analysis, the number of bulbs per pot was reduced by one each year.

When the anthers split, the flowers were removed and weighed ; the lengths of the flower stalks were recorded at the same time.

RESULTS.

Tulips.

Visual records.

The visual records of the tulips, summarized below, were similar in the preliminary experiment and in the first year of the three-year experiment. *Complete nutrient:* normal sturdy growth, good green colour ; large flowers on long stalks. *High nitrogen :* slightly earlier emergence ; temporary interveinal chlorosis in early stages of growth, otherwise normal. *Omitting nitrogen :* plants markedly less vigorous in first year and progressively so in succeeding years ; leaves small, pale green, and erect; early senescence of foliage ; flowering delayed, flowers small and slightly paler but stalks longer than normal (Fig. 1 f) ; bulbs reduced below flowering size by third year. *Omitting potassium :* no visual effects in first year ; slight reduction in size, with interveinal chlorosis followed by tip paling and scorch on lower leaves in second and third years (Fig. 1 e) ; emergence and flowering delayed by third year ; flowers smaller than controls in third year, stalks shortened, collapse of flower stalks above top leaf after " topping " in second and third years. *Omitting phosphorus :* growth reduced ; foliage dull green with purple tints ; flowering slightly delayed, smaller

flowers on shorter stalks than normal ; senescence slightly delayed. *Omitting calcium :* severe stunting and early death of foliage ; flowers smaller than normal ; collapse of stalk above top leaf at flowering in first year ; total physiological breakdown of bulb by end of second season and transverse splits in single stunted leaves (Fig. 1 a). *Omitting magnesium :* less vigorous growth ; interveinal chlorosis of older leaves followed by bleaching and pale necrotic spotting, finally by complete necrosis and early death of foliage (Fig. 1 c and d) ; flowering slightly delayed but blooms normal. *Medium calcium plus high manganese :* no apparent effects during first two years ; plants stunted with short flower stalks in third year ; senescence slightly advanced.

Table I.

Growth data on 5 cm. and 12 cm. tulip bulbs grown in sand culture; mean weight in g. per single parent bulb.

	Total wt. of bulbs		Wt. of main bulb		Mean no. of bulbs produced	
Size of parent bulb	5 cm.	12 cm.	5 cm.	12 cm.	5 cm.	12 cm.
Treatments :						
Complete nutrient	10·7	32·5	7·0	18·1	3·4	5·1
Omit N	4·6	23·1	3·5	12·8	2·4	5·0
Omit P	7·1	31·4	4·4	16·8	3·1	5·1
Omit K	7·0	29·3	4·9	17·5	3·1	4·8
Omit Ca	3·0*	11·6	2·0	11·5	2·3*	3·5
Omit Mg	5·3	21·8	3·4	13·4	3·3	4·8
Low Ca, high Mn	2·7	20·4	2·6	13·0	1·1	3·5

* 7 out of 10 bulbs killed.

Yields.

The bulb yield data are shown in Table I for the comparison of 5 and 12 cm. bulbs and in Table II for the three-year experiment with 7 cm. bulbs. In all treatments, bulb weight showed an increase over initial weight in the first year, though by widely differing amounts. In the three-year experiment those from the N, Ca and Mg deficiency treatments showed an increase of approximately only 50 per cent., whereas the complete nutrient bulbs increased by about 250 per cent.

In the second year, bulbs from all treatments except —P and —Ca showed some increase ; of these last, —P had remained at much the same weight as at the start of the season and —Ca had mainly undergone physiological breakdown. Where increases were recorded, only that of the —Mg bulbs was greater than in the previous year.

The increases in bulb weight during the third year were smaller than in the previous year with the complete nutrient, —K, —Mg and medium Ca plus high Mn, were the same with —N, and were greater with extra N and —P. The complete nutrient and extra N plants showed the greatest increases of about 130 per cent., —N, —K, —P and —Mg were all below 50 per cent., and the medium Ca plus high Mn treatment showed an increase of 70 per cent. Effects of N, Mg and Ca deficiencies were clearly the most drastic initially, irrespective of bulb size. Effects of P and K deficiencies were comparable with the others after three years. Differences between

treatments, and cumulative effects were mainly highly significant. The relative decreases in yield expressed as a percentage of that with the complete nutrient for each year are shown in Table IV.

TABLE II.

Yields (g.) and cumulative data for tulip bulbs grown in three-year experiments in sand culture.

	Year	Treatments								s.e.*
		Complete nutrient	Extra N	Omitting N	Omitting K	Omitting P	Omitting Ca	Omitting Mg	Low Ca High Mn	
Planting data										±
Mean weight of parent bulb	1	8·6	8·3	8·5	8·3	8·5	8·5	8·6	8·3	
	2	20·9	19·8	9·6	15·2	15·2	9·1	8·5	18·9	
	3	16·6	15·8	5·1	7·9	6·2	—	7·5	15·7	
Harvest data										
Mean total weight of bulbs	1	30·7	27·8	12·1	22·2	20·7	13·6	12·4	26·4	0·69
	2	50·7	43·6	11·6	20·7	14·5	—	19·1	44·7	
	3	38·6	35·4	6·1	9·8	7·2	—	9·8	26·8	
Cumulative effects	1+2	81·4	71·4	23·8	42·9	35·2	—	31·6	71·2	
" "	1+2+3	120·0	106·9	29·9	52·7	42·4	—	41·3	98·0	
Mean weight per bulb	1	9·0	10·1	5·2	7·2	6·8	5·2	4·3	8·8	0·37
	2	8·1	7·5	3·1	5·0	3·6	—	4·3	8·0	
	3	7·8	7·6	2·5	6·1	4·4	—	3·9	5·6	
Cumulative effects	1+2	8·4	8·3	3·9	5·9	4·9	—	4·3	8·2	0·22
" "	1+2+3	8·2	8·1	3·5	5·9	4·8	—	4·2	7·3	0·19
Numbers of bulbs per parent bulb	1	3·4	2·8	2·4	3·1	3·1	2·6	3·0	3·1	
	2	6·2	5·9	3·8	4·2	4·1	—	4·4	5·7	
	3	5·0	4·7	2·5	1·6	1·6	—	2·5	4·8	
Mean weight of largest bulb produced	1	23·5	22·6	10·4	16·9	16·7	10·8	9·3	20·5	0·49
	2	19·4	18·6	5·9	8·9	6·6	—	9·7	18·1	
	3	23·8	20·5	5·4	8·6	7·1	—	7·6	14·3	

* Differences exceeding 2 and 3 times the standard errors significant at 5 per cent. and 1 per cent. levels respectively.

DAFFODILS.

Visual records.

Complete nutrient : vigorous ; normal growth. *Extra nitrogen :* normal growth ; senescence slightly advanced. *Omitting nitrogen :* late emergence of shoots ; growth reduced ; foliage pale ; flowering delayed ; stalks slightly shorter but blooms normal; early senescence of foliage. *Omitting potassium :* growth slightly reduced ; stalks shorter but flowering otherwise normal ; early ripening of foliage. *Omitting phosphorus :* growth reduced ; flowering delayed ; short flower stalks ; early senescence. *Omitting calcium :* late emergence ; growth much reduced ; flowering delayed ; short flower stalks and small blooms ; early discoloration and collapse of foliage ;

breakdown of bulb tissues after second year. *Omitting magnesium :* plants slightly taller than normal ; early senescence of foliage. *Medium calcium plus high manganese :* no visual symptoms.

Table III.

Yields (g.) and cumulative data for daffodil bulbs grown in three-year experiment in sand culture.

	Year	Treatments								s.e.*
		Complete nutrient	Extra N	Omitting N	Omitting K	Omitting P	Omitting Ca	Omitting Mg	Low Ca High Mn	
Planting data										±
Mean weight of parent bulb	1	25·1	25·0	25·8	25·6	25·6	24·8	26·1	24·6	
	2	37·1	32·7	30·3	33·9	36·3	29·0	30·6	26·1	
	3	18·9	21·2	20·8	22·0	20·8	10·2	18·6	22·4	
Harvest data										
Mean total weight of bulbs	1	41·5	37·0	32·5	39·8	40·7	32·8	36·3	39·6	1·43
	2	62·0	48·1	34·3	56·4	47·6	—	43·1	54·8	
	3	36·8	40·9	22·5	28·8	28·0	—	26·4	39·6	
Cumulative effects	1+2	103·5	85·1	66·8	96·2	88·4	—	79·4	94·4	3·39
„ „	1+2+3	140·3	126·0	89·4	125·0	116·4	—	105·8	134·0	
Mean weight per bulb	1	41·5	37·0	32·5	39·8	40·7	32·8	36·3	39·6	1·43
	2	17·0	15·5	15·9	17·2	14·1	—	12·6	16·0	
	3	13·9	11·1	21·3	12·5	24·3	—	8·6	12·5	
Cumulative effects	1+2	22·2	20·7	21·1	22·4	20·2	—	18·0	21·3	
„ „	1+2+3	19·2	16·1	21·1	18·8	20·8	—	14·1	17·6	1·10
Numbers of bulbs per parent bulb	1	1·0	1·0	1·0	1·0	1·0	1·0	1·0	1·0	
	2	3·8	3·1	2·2	3·3	3·4	—	3·4	3·5	
	3	2·8	3·8	1·1	2·4	1·2	—	3·1	3·2	
Mean weight of largest bulb produced	1	41·5	37·0	32·5	39·8	40·7	32·8	36·3	39·6	1·43
	2	26·0	23·3	23·7	25·7	23·0	—	20·3	25·7	
	3	21·6	20·3	22·0	17·8	27·3	—	13·2	20·3	

* Differences exceeding 2 and 3 times the standard errors significant at 5 per cent. and 1 per cent. levels respectively.

Yields.

The bulb yield data are shown in Table III. In the first year the weight of bulbs with the complete nutrient, —K, —P and low Ca plus high Mn treatments increased about 50 per cent. over the weight of the original bulb. The lowest increase of 25 per cent. occurred with the —N treatment. The second year increases were slightly larger than in the first year with the complete nutrient, but with the other treatments remained about the same, or dropped. With the —Ca treatment, the weight did not increase but fell by about 25 per cent. A markedly greater increase occurred during the third year of the experiment from the complete nutrient and extra nitrogen treatments and to a smaller degree from the —P and medium Ca plus high Mn treatments. The increases in weight of bulbs from other treatments were

less than those of the previous year ; bulbs from the —N treatment again showed the smallest increase. Bulbs from the —Ca treatment underwent tissue breakdown during this year so that no weights could be recorded. The daffodil bulb results generally showed less variations than those shown by the tulips, and the general level of significance was also lower. The yields for each year are shown in Table IV as percentage decreases or increases relative to the complete nutrient treatment expressed as 100.

TABLE IV.

Decreases (—) or increases (+) in total yield per parent bulb relative to complete nutrient as 100 for each year.

Treatment ..	Extra N	—N	—K	—P	—Ca	—Mg	Medium Ca High Mn
Tulip, Year							
1	— 9·6	—60·6	—27·7	—32·6	—55·8	—59·6	—14·0
2	—14·1	—77·1	—59·2	—72·4	—	—62·4	—12·0
3	— 8·4	—84·2	—74·6	—81·4	—	—74·6	—30·6
Daffodil, Year							
1	—11·0	—21·8	— 4·7	— 2·2	—21·0	—12·7	— 4·7
2	—21·4	—44·7	— 9·2	—23·3	—	—30·5	—11·7
3	+11·0	—38·8	—21·8	—24·0	—	—28·3	+ 8·0

DISCUSSION.

An outstanding feature of the results was the marked difference between the tulip and the daffodil in their response to most of the mineral deficiencies, especially to deficiencies of nitrogen, magnesium and calcium in the first year. Analytical work now in progress may indicate whether this difference was related to initial mineral reserves and their subsequent uptake or translocation during each year's growth. Comparisons between the behaviour of 5 cm. and 12 cm. tulip bulbs in the preliminary experiment (Table I) suggest, however, that bulb size was at least one important factor in accounting for such differences.

A further distinction was that, whereas the tulip bulbs showed wide variations in weight of the largest bulb produced in different treatments, the daffodil bulbs were mainly fairly uniform until the third year. The effects of mineral deficiencies on the growth of the bulb were therefore relatively great for tulips in the first year but were much less for daffodils over the whole period of the experiments.

The large effects produced by deficiency of nitrogen were to be expected, but the equally marked effects of magnesium deficiency on tulips were not expected and the much slower responses to omissions of phosphorus or potassium were the more surprising. Ultimately these last two treatments had equally drastic effects on the tulips. The delayed effects of phosphorus and potassium deficiencies and their ultimate severity are clearly shown by the data in Table IV. Stoughton (9) found that phosphorus deficiency was the dominant factor in restricting bulb growth of the Dutch iris and that the phosphorus effect was marked after a single year's growth. The effect of nitrogen deficiency, however, was much less, in contrast to the impor-

PLATE I

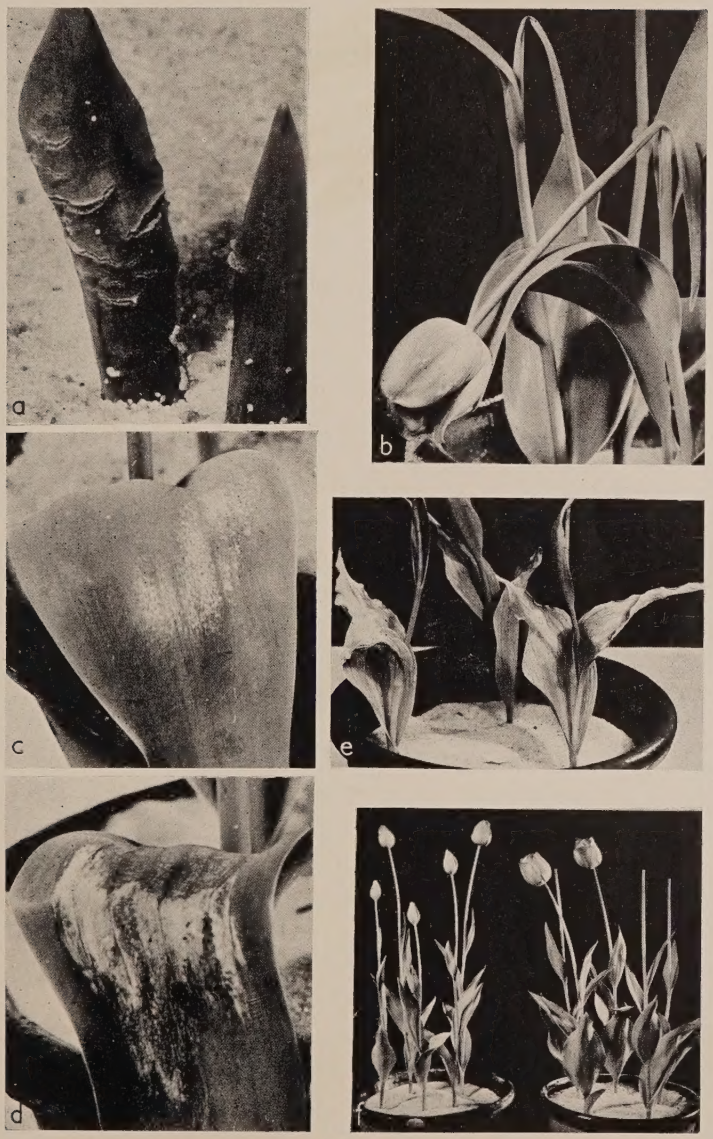

Fig. 1.

a Effects of severe calcium deficiency in tulip causing transverse splits in first leaf.
b " Topple " in both " headed " and uncut flower stems due to calcium deficiency.
c Early symptoms of magnesium deficiency in tulip.
d Advanced symptoms of magnesium deficiency.
e Scorching caused by potassium deficiency.
f Effect of nitrogen deficiency on habit (left) compared with growth in complete nutrient (right).

[face page 242

tance of nitrogen deficiency for tulip in our experiments in spite of the greater weight of the tulip as compared with the Dutch iris bulbs.

Omission of nitrogen caused similar effects in extra length of flower stems and delay in flowering in both tulip and Dutch iris (9). In both experiments the number of bulbs produced from a single parent was mainly independent of treatment after one year, but cumulative effects due to omission of N, P, K or Mg might be inferred for the tulip, as shown by Table II. Mean weight per bulb was reduced by most treatments for tulip but not for daffodil which corresponded more closely to the Dutch iris (9) in this respect.

The results obtained by Bould (1) for tulip were similar in some respects to those reported here, namely a total yield response to nitrogen in the first year and to phosphorus, and to a lesser extent to potassium in the second year. Omission of nitrogen also delayed flowering and resulted in smaller, paler blooms, but stems were shorter in all treatments including nitrogen deficiency.

Neither plant could be regarded as a generally useful indicator crop, and no readily recognizable visual symptoms were recorded for the daffodils. Tulips were visually the more responsive of the two, and the effects of magnesium deficiency and of calcium deficiency illustrated in Plate I were fairly specific. The collapse of the tulip flower stalks under conditions of moderate calcium deficiency suggests that this factor is the cause of the " topple " described by Moore (8). This is in agreement with the conclusions of Uyldert (10) in Holland. The collapse of petioles or pedicels at flowering has been recorded in such other plants as flax, clovers, pea and rape suffering from calcium deficiency (3, 4, 5). It was interesting, however, that in the first year of the main experiment the " topple " occurred in stems of several plants some days after removal of the blooms at a time when no external abnormality of the flower stems was evident. A " topple " effect also occurred in the potassium-deficient plants in the third year. No " topple " occurred in the daffodils given similar treatments. 5 cm. tulip bulbs were killed by —Ca in the first year in the preliminary experiment, and calcium deficiency was comparable in importance to deficiency of nitrogen or magnesium.

The tolerance to excess manganese shown by both species suggests that this factor in the acid soil complex may not be of much importance in the growth of either under acid conditions. There is no information at present on the effects of aluminium.

The supply of nitrogen at twice the normal level was not beneficial either for total yields or for the " build up " of the main bulb in contrast with other crops, e.g. brassicas, which respond well to additional nitrogen under similar conditions in sand cultures at Long Ashton.

SUMMARY.

1. Tulip (variety Rose Copland) and daffodil (variety King Alfred) bulbs were grown in sand cultures, with a complete nutrient, extra nitrogen, deficiencies of N, P, K, Ca, Mg and with excess Mn.

2. Effects of mineral deficiencies were greater on tulip than on daffodil, and were greater for 5–7 cm. than 12 cm. tulip bulbs.

3. Tulips were most sensitive to deficiencies of nitrogen, magnesium and calcium

in the first year. Phosphorus and potassium deficiencies had marked effects in the second and third years respectively.

4. Calcium deficiency in tulips caused an effect similar to " topple " in the first year and breakdown of the bulbs in the second year. Potassium deficiency also caused a similar " topple " effect in the third year.

5. Calcium deficiency produced no " topple " effect in daffodil but caused breakdown of the bulbs in the second year.

6. Increases in bulb weight were least in tulips grown without N, Mg or Ca and least in daffodils grown without N or Ca in the first year. Omission of P had comparable effects on tulip and omission of P or Ca had nearly comparable effects on daffodil in the second year. Omission of K had comparable effects on both in the third year.

ACKNOWLEDGMENT.

We would like to thank Dr. H. V. Taylor, C.B.E., V.M.H., Chairman, and the members of the Bulb Sub-committee of the Agricultural Improvement Council Horticultural Experiments Committee for their interest in this work and for permission to publish it.

REFERENCES.

(1) *Bould, C.* (1939). Studies on the nutrition of tulips and narcissi. J. Pomol., **17,** 254.

(2) *Handley, F. W.* (1933). Manuring of tulips ; Report on experiments with bulbs, Kirton Farm Institute and Experiment Station, Kirton, 1933.

(3) *Hewitt, E. J.* (1944). Experiments in mineral nutrition. 1. The visual symptoms of mineral deficiencies in vegetables and cereals grown in sand cultures. Progress report No. 1. Ann. Rep. Long Ashton Res. Sta., 1943, 33.

(4) ——— (1945). Experiments in mineral nutrition. 2. The visual symptoms of mineral deficiencies in crop plants grown in sand cultures. Progress report No. 2. Ann. Rep. Long Ashton Res. Sta., 1944, 50.

(5) ——— (1946). Experiments in mineral nutrition. 3. The visual symptoms of mineral deficiencies of crop plants grown in sand culture. Progress report season 1945. Ann. Rep. Long Ashton Res. Sta., 1945, 44.

(6) ——— (1952). A biological approach to the problems of soil acidity. Internat. Soil Sci. Soc. Dublin meeting Comm. I and II Trans., **1,** 107.

(7) ——— (1952). The use of sand and water culture methods in the study of plant nutrition. Tech. Commun. Bur. Hort. E. Malling. **22.**

(8) *Moore, W. C.* (1939 and 1949). " Diseases of bulbs." Ministry of Agriculture and Fisheries, London. Bull. No. 117, 37.

(9) *Stoughton, R. H.* (1940). The nutrition of the Dutch iris : an experiment in factorial design. J. Pomol., **18,** 297.

(10) *Uyldert, I. E.* (1934). A physiological tulip disease. Proc. Linn. Soc. London, 1933-4, pt. III, 95.

(*Received* 21/11/53.)

DAMPING-OFF OF TOMATO BY SPECIES OF *PYTHIUM* AND ITS CONTROL BY USE OF FORMALIN DUST

By NANCY MONTGOMERY
Formerly Plant Pathology Laboratory, Imperial College, London

UNDER glasshouse conditions the damping-off of tomatoes is mainly ascribed to species of *Phytophthora*, in particular to *P. parasitica* Dastur or *P. cryptogea* Pethyb. & Laff. Once introduced, by way of compost or water supply, they soon build up unless eliminated by soil sterilization. Species of *Pythium*, though they have been recorded from time to time as causing damping-off of tomatoes in various countries, have received little attention in Britain in this connection. For instance, they are not mentioned as affecting this crop in Bewley's " Diseases of Glasshouse Plants " (1923) or in Bulletin No. 77 on " Tomatoes " (Anon., 1948) or Bulletin No. 123 on " Diseases of Vegetables " (Ogilvie, 1948) of the Ministry of Agriculture and Fisheries. Nevertheless, as will be shown below, species of *Pythium* which are able to cause serious damping-off of tomato seedlings under suitable conditions are liable to occur in ordinary soils or composts, independently of their having previously grown tomato crops. The use of properly sterilized soil safeguards against loss by damping-off, whether caused by *Phytophthora* spp. or by *Pythium* spp. As the latter are much the more widely prevalent in nature, they are more likely to affect the private gardener or the small-scale grower who lacks adequate facilities for sterilizing his composts by heat and preserving them in that condition. The two species of *Phytophthora* which are of chief importance to tomato cultivation in Britain are high temperature organisms, causing most damage within the temperature range 25–30° C., whereas the *Pythium* species are most active at lower temperatures. Thus a lowering of temperature to below 20° C., which is recommended as a palliative measure for dealing with tomato damping-off or foot-rot caused by *Phytophthora* species, merely accentuates the trouble if it is due to *Pythium* species. Accordingly it is of some importance to distinguish between these two types of damping-off disease.

The object of this investigation was to examine a number of ordinary soils, i.e. such as had no known previous history of tomato cultivation, with respect to their liability to cause damping-off of tomato seedlings, to isolate the fungi concerned, to determine the effect of environmental conditions on intensity of disease, and finally to test the efficiency of formalin, applied to the soil in the form of an easily prepared and handled dust, for control of the disease.

ISOLATIONS FROM DAMPED-OFF SEEDLINGS.

Seed of tomato, variety Early Market, used throughout this work and taken from healthy fruit of the year before, was sown in five soils of various textures taken from the field (Slough Field Station) and in a grower's compost. Germination was in a cool greenhouse at various times of the year, and from time to time there was considerable pre- or post-emergence damping-off in all the soils. Isolations were made in the usual manner from diseased seedlings (cotyledons, hypocotyl, and roots) ; typical data for three of the soils are summarized in Table I.

TABLE I.

Isolations from damped-off seedlings.

Soil type	Total plants	*Pythium debaryanum*	*Pythium intermedium*
Peaty	20	0	14
	10	0	8
	18	0	18
	30	0	27
Medium loam	31	31	0
	18	17	0
	27	27	0
Grower's compost	7	0	6
	78	0	65

The above results were confirmed in numerous isolations made from time to time in the course of the work, the dominant isolate being one or the other of the two species of *Pythium* cited. Occasionally cultures of *Fusarium* and *Alternaria* were obtained, but it is striking that *Rhizoctonia solani* occurred only once, and *Phytophthora* not at all.

As illustrated in Table I, only one species of *Pythium* was detected in each soil type. The possibility, however, that the other species was present in small proportion cannot be excluded, as the large number of isolation plates handled made it impracticable to explore each culture in detail. The identification of one isolate as *P. debaryanum* Hesse is based on essential agreement with the description given by Middleton (1943), with the exception that it was not seen to produce zoospores. The culture which was provisionally identified as *P. intermedium* de Bary produced catenulate sporangia in great abundance but no oospores were seen. The two species differed distinctly in their response to temperature : on cornmeal agar *P. intermedium* had its optimum for linear growth in the range 20–25° C., as against 30–35° C. for the other.

For purposes of comparison an isolate of *Phytophthora parasitica* was taken from a diseased tomato plant received at the laboratory ; neither this nor one obtained from the Commonwealth Mycological Institute produced oogonia, but when grown together they give oogonia with amphigynous antheridia and later oospores of dimensions agreeing with those recorded by Dastur (1931). It is possible that the isolate used in this work is heterothallic, in accordance with the claim of Thomas and Ramakrishnan (1948) regarding this species.

That the isolates obtained from damped-off seedlings in the course of this work came from the soil and not from the seed itself was shown by the absence of damping-off in heat-sterilized soil.

Effect of temperature and soil moisture on amount of disease

For this work soil was sterilized by steam or by electric heating at least two weeks before it was inoculated. Sand-cornmeal cultures (100 g. sand, 2 g. cornmeal, 35 ml. water) were kept at 25° C. for three weeks after inoculation. Sterilized soil, at the required percentage of water-holding capacity (% W.H.C.) was inoculated from this culture on the basis of 2 per cent. by weight and incubated at 18–25° C. in

covered storage tins. These were kept at constant weight, though little change in water content took place over several months under these conditions. Five to ten replicates of twenty-five seeds were used for each treatment.

Table II shows the effect of temperature and soil moisture on pre- and post-emergence damping-off of tomato seedlings in soils artificially inoculated with *Pythium intermedium* and with *Phytophthora parasitica*. The data of survival were recorded at the second rough-leaf stage of the plants. The inoculated soils, set up at 30 per cent. W.H.C., had been allowed to incubate at 25° C. for six weeks before the seed was sown. At the time of sowing, samples were adjusted to 30 per cent. and 45 per cent. W.H.C. Uninoculated controls in this experiment gave figures for emergence and survival ranging between 94 and 98 per cent.

TABLE II.

Effects of temperature and soil-moisture content on damping-off by Pythium intermedium *and* Phytophthora parasitica.

% W.H.C.	*Pythium intermedium*				*Phytophthora parasitica*			
	16° C.		25° C.		16° C.		25° C.	
	% Emerg.	% Surv.	% Emerg.	% Surv.	% Emerg.	% Surv.	% Emerg.	% Surv.
30	22	13	92	86	90	90	16	15
45	28	2	94	83	89	76	41	36

A clear-cut effect of temperature is shown at both water contents, *Pythium intermedium* being much more active at the lower than at the higher temperature, and *Phytophthora parasitica* behaving conversely. Beyond a suggestion that both fungi gave lower survival at 45 per cent. than at 30 per cent. W.H.C., the effect of the latter factor was not noticeable. When, however, as was shown in further experiments, the water content was raised to 70 per cent. W.H.C., survival was distinctly reduced at all three temperatures used (15° C., 20° C., 25° C.).

The contrasting response to temperature of *Pythium intermedium* and *Phytophthora parasitica* was regularly confirmed in repeat experiments, though the general level of attack varied somewhat from one experiment to another, even under apparently the same conditions.

A similar comparison between the two species of *Pythium* is given in Table III. The uninoculated controls in this experiment showed 97–100 per cent. survival. All treatments were maintained at 35 per cent. W.H.C.

TABLE III.

Effect of temperature on damping-off by two Pythium *species.*

Temperature ° C.	*P. debaryanum*		*P. intermedium*	
	% Emerg.	% Surv.	% Emerg.	% Surv.
16·5	100	0	100	5
27·0	100	0	98	63
30·0	96	4	99	96

The effect of temperature on attack by *P. intermedium* is similar to that shown in Table II ; with *P. debaryanum* attack is drastic over the whole temperature range. On the other hand, in a soil naturally infected with *P. debaryanum*, and presumably with a concentration of the fungus less than was used in the experiment of Table III, the percentage survival was 65 at a temperature which fluctuated round 25° C., as against 37 at 15° C. With both species, therefore, incidence of disease decreases at higher temperatures, though the effect is much more distinct for *P. intermedium*. This behaviour is in accordance with the lower optimum temperature for growth shown by this fungus.

TABLE IV.

Effect of temperature and water content on damping-off in natural soils.

Soil	% W.H.C.	15° C.		30° C.	
		% Emerg.	% Surv.	% Emerg.	% Surv.
1	30	71	52	91	84
	60	56	36	72	50
2	30	83	48	92	83
	60	40	29	52	40
3	30	69	41	94	86
	60	54	42	82	62
4	30	66	55	80	75
	60	73	52	76	69

Throughout the experiments on the use of formalin dust to be described later, the temperature and water content factors were often varied in order to test the efficiency of the treatment under different conditions. Untreated controls were necessary for these experiments, and these provided extensive data bearing on the effect of temperature and water content upon intensity of disease, both with naturally contaminated and artificially inoculated soils. Illustrative results are given in Tables IV and V for naturally contaminated soils, the former showing a lower level of attack than the latter.

Emergence and survival were invariably higher at 30° C. than at 15° C. ; at both temperatures, and more distinctly at the higher one, emergence and survival were lowered in the wetter soil.

TABLE V.

Effect of temperature on damping-off in natural soils.

Soil	15° C.		23° C.	
	% Emerg.	% Surv.	% Emerg.	% Surv.
1	20·3	7·5	50·7	43·0
2	20·0	10·5	69·0	60·5

In both soils of Table V, emergence and survival were poor and especially so at the lower temperature.

The broad result of this section is that damping-off of tomatoes by the two *Pythium* species is accentuated by low temperature and, though less prominently, by high soil moisture. This is in agreement with the statement of Alexander, Young and Kiger (1931) on the behaviour of *Pythium ultimum*. On the other hand there is general agreement that *Phytophthora* species are more active on tomato seedlings at higher temperatures, as has been confirmed here for *P. parasitica*. Thus Sarejanni (1937), working in Greece, stated that the collar rot of tomatoes and other Solanaceous plants required a temperature of over 28° C. before the disease became epidemic, and that it was reduced if the temperature fell below 25° C. Similarly Bewley (*loc. cit.*, p. 62) recommends lowering the greenhouse temperature to mitigate the damage by *Phytophthora* species.

MODE OF INVASION BY *Pythium* SPECIES.

In the course of making isolations at various phases of the work, two contrasting modes of invasion were noted. In the first type, which was usually seen when the temperature of germination was rather high (*c.* 25° C. upwards), the plants in contaminated soil emerged in the usual manner but, after a time, began to lag behind those in clean soil. The roots of the former showed small brown lesions or dead portions, and from such damaged rootlets isolates of *Pythium* were easily obtained. When the root systems of such plants were carefully washed free of soil and compared with those of perfectly sound plants, they were demonstrably less extensive than the

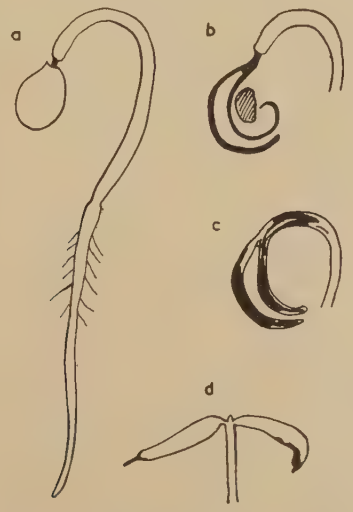

FIG. 1.

Appearance of diseased seedlings germinated in natural soil. Diseased parts shown in black. (*a*) Seedling with sound root system and cotyledons still enclosed in testa. (*b*) Part of same seedling with testa removed. Cotyledons severely attacked. (*c*) Seedling showing lesions on cotyledons and hypocotyl. (*d*) Seedling with slight attack on cotyledons.

latter and did not show up so uniformly white. Hence the lag in growth of the stem parts as mentioned.

In the second type, which generally occurred at lower temperatures (*c.* 15° C. downwards) and which was accompanied by reduced emergence and survival, the cotyledons were found to be attacked while still within the testa, the disease spreading from these down the hypocotyl. Often the cotyledons remained in the soil, still enclosed by the testa, and the seedling died. Such as survived often showed distorted cotyledons with black lesions. Fig. 1 illustrates various grades of this mode of attack. These effects did not arise from seed-borne contamination, for similar seed germinated in steam-sterilized soil gave a full complement of plants with healthy cotyledons. As temperature appeared to be the chief determining factor, its effect was examined in greater detail, as follows.

Tomato seed, after sterilization with 1 per cent. formalin for 5 minutes and washing in water, was put to germinate in Petri dishes at 18° C. Seed or seedlings at various stages of development, viz. after 1, 3, 4, 5, 6 days, were transferred to the surface of plain agar and inoculated with *Pythium intermedium* hyphae from 3-day-old cultures on oatmeal agar. For each treatment, as for uninoculated controls, 10 seeds or seedlings were used. The batches were then incubated at the temperatures shown in Table VI, which contains a summary of the results. All the controls remained sound.

TABLE VI.

Effects of temperature and stage of seedling development on attack by Pythium intermedium.

Days' germination before inoculation	Length of radicle (mm.) at inoculation	Temperature after inoculation					
		15° C.		20° C.		27·5° C.	
		Length of radicle (mm.)	No. diseased	Length of radicle (mm.)	No. diseased	Length of radicle (mm.)	No. diseased
1	0	1	10	2	10	2	10
3	0	1	10	2	10	40	2
4	2	5	10	3	10	40	1
5	4	6	10	40	4	40	0
6	15	15	4	40	1	40	0

Fig. 2 illustrates the appearance of sample seedlings under the various treatments, affected regions being shown in black (except where the cotyledons are hidden within the seed coats).

Attack was most severe on seed inoculated before emergence of the radicle and, at this stage, all seedlings were liable to be killed at all temperatures over the range examined. Seedlings inoculated after 3–5 days' germination (at 18° C.) succumbed to attack at 15° C., to a less extent at 20° C., and grew normally at 27·5° C. apart from slight lesions on a few plants, even though the inoculum grew and sporulated

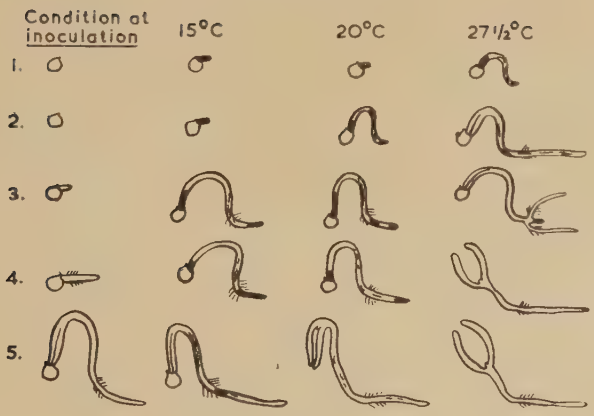

FIG. 2.
Appearance of seedlings inoculated with *Pythium intermedium* on agar at 15°, 20°, 27·5° C. at various intervals (1–5 days) after being set out to germinate.

round the seedlings at all three temperatures. Seedlings inoculated after 6 days' germination, by which time the cotyledons were beginning to emerge from the seed coats, were only slightly attacked at all temperatures and they continued to grow normally.

From these results it is seen that *Pythium intermedium* is able to kill tomato seedlings over the whole range 15–27·5° C. provided that it gains access sufficiently early to the young plant. Once germination has begun, the amount of damage produced is less, and this stage of resistance or disease-escape is more quickly reached the higher the temperature. The percentage of plants killed in the early highly susceptible stage would obviously depend upon the concentration and condition of fungal mycelium in the soil at the time when the seed is sown.

CONTROL OF DAMPING-OFF BY FORMALIN DUST.

The work described in this section arose out of earlier investigations in this laboratory by Tandon (1939) and Deshpande (1940) who tested a large number of chemical substances, recommended at one time or another, for the control of damping-off. Among the substances examined were potassium permanganate, sulphuric acid, acetic acid, ortho-oxyquinoline sulphate, several chloronitrobenzenes, Cheshunt Compound, and formalin in liquid or dust form ; the tests were made with tomato seed sown in garden soil which had been inoculated with *Phytophthora cryptogea*. In many of the experiments the inoculum potential was so high that emergence in the controls was reduced to zero. Under these drastic conditions the only reagents which gave a high measure of control, both as regards good emergence and continued survival, were formalin solution (2 per cent.) and formalin dust. The latter was prepared according to the formula of Alexander, Young and Kiger (1931) with the simplification that diatomaceous earth as absorbent was replaced by ordinary dried soil. As formalin dust is convenient to prepare and handle, the writer's experiments were restricted to its use and further evaluation.

Commercial formalin (40 per cent. formaldehyde) was absorbed on sieved air-dried soil in the proportion of 15 : 85 parts by weight. This dust was then stored in air-tight jars and used soon after being made up. For use, the appropriate quantity—0·4 to 2·4 parts of the stock preparation—was added to 100 parts of soil, well mixed in ; the sowings were made immediately, the seed being covered with the same soil. The pots (5-in.) or seed boxes (5 in.×5 in.×2 in.) were packed closely on the bench and covered with glass plates until emergence occurred. Under these conditions the loss in weight by evaporation was less than 1 per cent. at temperatures up to 20° C. Four or more replicates per treatment were used, and seed was sown thinly, viz. 20–50 per box, so that the seedlings could be carried if necessary to the fourth rough-leaf stage without overcrowding. For tests under more controlled conditions, circular glass dishes (2½ in.×1½ in.) were used. The latter experiments, carried out in incubators, were usually terminated when the cotyledons had come above ground.

Experiments were carried out throughout the year and at various temperatures and soil-moisture levels. A variety of naturally contaminated soils was available and tests were also made with soils artificially inoculated (by the method described on p. 246) with active cultures of the following : *Pythium intermedium*, *P. debaryanum*, *Phytophthora parasitica* and *Rhizoctonia solani*. From the large mass of concordant data so obtained, it will be sufficient here to quote a number of experiments as illustrating various points.

Table VII shows the effect of 0·4 per cent. formalin dust added to a number of naturally contaminated soils. The Table gives the survival figures up to the second rough-leaf stage and the average time, over the various replicates, for 50 per cent. of the seedlings under any particular treatment to emerge. In this experiment the average greenhouse temperature was 14° C.

TABLE VII.

Effect of 0·4 per cent. formalin dust on survival and period of emergence of tomato seedlings in soils naturally contaminated with Pythium *sp.*

Soil type	Control		0·4% formalin dust added	
	% Surv.	Average emergence period (days)	% Surv.	Average emergence period (days)
Peaty	27	12	78	13
Medium loam	40	10	78	10
Heavy loam	50	10	85	10
2 Loam+1 peat+1 sand	33	13	76	17
Grower's compost	40	10	88	11

The treatment gave substantial control of damping-off in all the soils. In four of them the formalin treatment gave little or no check (0–1 day) to emergence ; on the other hand in the loam-peat-sand mixture, which was of light texture, a check of 4 days was recorded. However, by the time the seedlings had reached the second rough-leaf stage those in treated soils had overtaken the controls. Four weeks after emergence, batches of plants were pricked out into steam-sterilized soil, and the average length of stem from apex to insertion of cotyledons measured after another

4 weeks, by which time about 7 rough leaves were showing. The results were :

Average height above cotyledons, Controls .. .. 7·1 cm.
Formalin-treated .. 8·3 cm.

The difference shown was significant at the 20 : 1 level. This result rests upon the protective effect of formalin dust on the root system.

In contrast to Table VII, in which damping-off was severe in the controls, Table VIII shows the effect of formalin dust under conditions of more moderate attack. The data of survival and mean height were taken 4 weeks after sowing, and the height is, as before, the measurement from insertion of cotyledons upwards.

TABLE VIII.

Effect of formalin dust on survival, period of emergence and subsequent growth of tomato seedlings.

Soil type	Control			0·6% form. dust			1·2% form. dust		
	% Surv.	Average emerg. period (days)	Mean height cm.	% Surv.	Average emerg. period (days)	Mean height cm.	% Surv.	Average emerg. period (days)	Mean height cm.
Loam	83	8	3·0	95	10	4·2	96	13	3·2
2 loam+1 sand ..	77	8	2·7	89	12	1·9	89	15	0·9

Sig. diff. between mean heights : 1·3 for P=0·05 ; 1·8 for P=0·01.

Both doses of the fungicide materially increased the stand of plants, but there was a distinct check to emergence, especially with the higher dosage. Also, in agreement with Table VII the check was intensified by mixing sand with the soil used. At the time when the heights of the plants were recorded, the plants in loam treated with 0·6 per cent. formalin dust had outstripped the controls (Diff. nearly signif. at 20 : 1 level) ; those treated with the higher dose had just caught up with the controls. In the loam+sand mixture the severer initial check was still in evidence after 4 weeks, and was significant at the 100 : 1 level in the batch germinated in

TABLE IX.

Effect of watering before sowing on survival and emergence period, with or without formalin dust.

Soil		Control		Formalin dust			
				0·6%		1·2%	
		% Surv.	Emerg. period	% Surv.	Emerg. period	% Surv.	Emerg. period
Peaty	watered ..	27	7	91	7	83	9
	non-watered	52	7	78	8	57	14
Loam+peat+sand	watered ..	40	6	92	9	81	9
	non-watered	66	9	53	18	0	8

presence of 1·2 per cent. formalin dust. In this experiment, treatment with 0·6 per cent. of the dust is probably too high for the best all-round result, and treatment with 1·2 per cent. represents a considerable overdose.

It is common practice to water pots and seed boxes before sowing. Table IX gives a comparison of the effect of formalin dust in soils watered or unwatered.

In the controls, watering diminished the stand of plants ; with formalin treatment, on the other hand, it had a beneficial effect both on survival and speed of emergence, probably because the watering carries much of the formalin down to the bottom of the seed boxes, but not before it has effected a beneficial sterilization of the upper soil layers. The effect of watering is particularly well shown in the two comparisons in the bottom right-hand corner of Table IX where the combination of light soil mixture, comparative dryness, and overdose of fungicide led to complete failure of emergence. The desirability of watering before sowing is also stressed by Wilson and Tilford (1933).

Numerous tests were made with 0·4 per cent. formalin dust in soils artificially contaminated with the common damping-off species. The conditions were adjusted, mainly by means of temperature, so as to give various intensities of damping-off in the controls. A list of results so obtained follows, the figures denoting percentage survival ; the first figure of each pair is that of the control :

Pythium intermedium : 5, 100 ; 9, 95 ; 39, 76 ; 39, 80 ; 63, 100 ; 75, 86 ; 76, 95 ; 96, 100.

P. debaryanum : 0, 96 ; 0, 100 ; 4, 100.

Phytophthora parasitica : 10, 95 ; 16, 99 ; 84, 96.

P. cryptogea : 0, 88 ; 49, 76.

Rhizoctonia solani : 51, 57.

Invariably a high degree of control was obtained with *Pythium* and *Phytophthora* species. On the other hand the treatment was of little or no value against *Rhizoctonia solani*.

Altogether the experiments have shown that formalin dust (0·4 per cent.) gives an effective control of tomato damping-off as caused by *Pythium* and *Phytophthora* species. A small but evanescent check to emergence may be caused, especially when the soil of the seedbed is light in texture. The danger of a check can be largely eliminated, even with an overdose of the fungicide, by watering the seed boxes immediately before the seed is sown.

These beneficial results have been obtained in all cases with seed boxes or pots covered with glass plates to maintain surface moisture up to the time of seedling emergence. The covers would also slow down the escape of formaldehyde. That this method succeeds with tomatoes is no doubt to be attributed to the comparatively slow rate of germination, so that much of the fungicidal gas has escaped while the embryo is still within the seed coat. With more rapidly germinating seed, such as lettuce or brassicas, the procedure described is quite unsafe.

Whereas tomato seed can safely be sown in soil to which 0·4 per cent. formalin dust has been added immediately before sowing, the same is not true for tomato seedlings pricked out into freshly treated soil. The majority of the seedlings would be killed by this treatment. With soils contaminated by *Pythium* species, protection of the pricked-out seedlings may not be so necessary, because they have by this time passed the stage of high susceptibility (*vide* Fig. 2), and if the temperature is raised to

the neighbourhood of 25° C. damage is negligible. With *Phytophthora* species, however, which attack strongly at higher temperatures and which are more associated with post-emergence damping-off and with foot-rot of larger plants, protection in the seedbed only gives little benefit in the long run. Treatment of the potting soil is also necessary.

The time required for adequate aeration obviously depends on factors such as temperature, amount of soil, ventilation, etc. Thus in a prepared soil containing 0·4 formalin dust and placed at once in small pots (3-in.) or shallow seed boxes, one day's aeration at *c.* 22° C. was sufficient, as against 4 days at 15° C. Table X gives the results of two experiments in which tomato seedlings were pricked out into soil, untreated or treated with formalin dust (0·4 per cent.). Equal numbers of plantings were made into control soil and soil previously inoculated with *Phytophthora parasitica.*

TABLE X.

Effect of airing period on survival in soil treated with formalin dust.

Experiment	Aeration temp, ° C.	Aeration period. Days	Control soil		Soil inoculation *P. parasitica*	
			No F.D.	0·4%F.D.	No F.D.	0·4%F.D.
I. 24 plants per treatment	16	4	24	24	0	24
	32	2	24	24	0	24
II. 45 plants per treatment	16	2	45	25	18	25
	20–35	2	45	25	0	25

In the first experiment, 4 and 2 days' aeration at 16° C. and 32° C. respectively were sufficient, and in the inoculated soil the formalin dust gave complete protection under conditions where all the seedlings died in its absence. In the second experiment, the results were less satisfactory, the behaviour of the seedlings in the control soil showing that aeration had been insufficient. In the inoculated soil, the formalin dust gave as good a stand as in the control soil similarly treated.

CONCLUSIONS.

Some species of *Pythium,* in virtue of their general saprophytic nature, are normal inhabitants of certain soils, in which respect they differ from many *Phytophthora* species which are more specialized to the parasitic mode of life and which therefore require the presence of suitable host plants for their perpetuation. *Pythium debaryanum* and *P. intermedium* are two widely prevalent species, and both are capable of strongly attacking tomato seedlings, especially when germination has taken place at a somewhat low temperature and in presence of high soil moisture. On the other hand, *Phytophthora parasitica,* which is the best known species of that genus attacking tomato plants, is more active at high soil temperatures. For this reason and also because its attack is not limited to the early life of the plant, it is a source of danger even in properly managed nurseries, because it may gain access to heat-

sterilized beds and there find conditions suitable for its activity. In such nurseries species of *Pythium*, if introduced, would be much less likely to cause damage.

On the other hand it is to the small grower and to the amateur gardener that *Pythium* species are likely to be troublesome. Unsterilized or inadequately sterilized composts or ones which have become contaminated after sterilization are often used, and control of temperature in the early spring months when seed is sown may be haphazard. It is probable, therefore, that, in spite of the negligible attention which has been paid to *Pythium* species in English tomato growing, a considerable aggregate loss arises from this cause. The formalin dust method which was first described from the United States by Alexander, Young and Kiger (1931) and which has been tested in great detail in the experiments reported here, offers a cheap and effective method of dealing with tomato damping-off disease. The fungicide in the form of a dust has the merit that it can be readily and uniformly incorporated in the soil and that it can be applied in such a way as to interfere very little with the normal operations of cultivation.

SUMMARY.

1. Isolations from damped-off tomato plants showed the prevalence of *Pythium debaryanum* and *P. intermedium* in a number of garden soils or composts.

2. Both fungi, and especially *P. intermedium*, while they can be very destructive at low temperatures (*c.* 15° C. and less), are relatively inactive at temperatures exceeding 20° C. *Phytophthora parasitica* behaves conversely in this respect. High soil moisture also favours attack by the *Pythium* species.

3. The characteristic mode of invasion by the *Pythium* species is *via* the cotyledons, and the phase of highest susceptibility is while these are still contained within the seed coat. In this way considerable pre-emergence damping-off may occur at lower temperatures. Later there is damage to the roots, the less the higher the temperature.

4. Substantial control of damping-off by *Pythium* (and *Phytophthora*) species is given by incorporation of a small quantity (e.g. 0·4 per cent.) of concentrated formalin dust (15 g. formalin to 85 g. air-dried soil). This method is easily applied at the stage of seed sowing and, with certain precautions, also when the seedlings are being pricked out.

ACKNOWLEDGMENT.

I am indebted to Professor W. Brown, F.R.S., who suggested the investigation, and who prepared the text for publication.

REFERENCES.

Alexander, L. J., Young, H. C., and *Kiger, G. M.* (1931). Causes and control of damping-off of tomato seedlings. Ohio Agric. Exp. Sta., Bull. 496, 38 pp.

Anon. (1948). Tomatoes : cultivation, diseases and pests. Min. Agric. & Fisheries, Bull. 77.

Bewley, W. F. (1923). Diseases of glasshouse plants. Ernest Benn Ltd., London.

Dastur, J. F. (1931). *Phytophthora parasitica.* A new disease of castor-oil plants. Indian Dep. Agric. Mem., Bot. Serv., **5,** 177-231.

Deshpande, R. S. (1940). A study of conditions which influence the persistence of certain Phycomycete parasites in soil. Ph.D. Thesis, London University.

Middleton, J. T. (1943). The taxonomy, range and geographical distribution of the genus *Pythium.* Mem. Torrey Bot. Club, **20,** 1-171.

Ogilvie, L. (1948). Diseases of vegetables. Min. Agric. & Fisheries, Bull. 123.

Sarejanni, J. A. (1937). Collar-rot of cultivated Solanaceae and the classification of the genus *Phytophthora.* Abs. in Rev. appl. Mycol., **16,** 833.

Tandon, R. N. (1939). Control of damping-off of tomato. Ph.D. Thesis, London University.

Thomas, K. M., and *Ramakrishnan, T. S.* (1948). Studies in the genus *Phytophthora.* II. Indian Acad. Sci., Sect. B, **27,** 55-73.

Wilson, J. D., and *Tilford, P. E.* (1933). Use of formaldehyde dust in growing seedlings. Ohio agric. Exp. Sta., Bull. 520, 40 pp.

(*Received* 28/12/53.)

THE EFFECTS OF DIFFERENT WATER-REGIMES ON THE GROWTH OF PLANTS UNDER GLASS

I. EXPERIMENTS WITH TOMATOES (*LYCOPERSICUM ESCULENTUM* MILL.)

By P. J. SALTER
Department of Horticulture, University of Nottingham School of Agriculture, Sutton Bonington

VALUABLE information regarding the water relations of crop plants can be obtained by growing them under different and definable water-regimes. Shantz (1927) pointed out the impossibility of maintaining soil at any uniform moisture content lower than field capacity, but the concept of a reproducible water-regime appears to have been due originally to Veihmeyer (1927) who suggested that it was possible for the moisture content of a soil to be allowed to fluctuate only through a definable range. For comparative purposes, different water-regimes may be maintained by allowing some soils in a series to dry to a lower moisture content than others before they are watered, provided that they are always re-wetted to field capacity and to a specified depth at each watering.

The effectiveness of using different water-regimes for the study of plant/water relationships depends upon the degree of accuracy with which they can be maintained. This will depend, amongst other factors, upon the method used for determining the " critical dry point ", i.e. the limit to which the soil is allowed to dry and also the way in which the quantity of water used at each application is determined. Various investigators have used techniques of sampling and drying (Veihmeyer, 1927), soil moisture tensiometers (Ayers, Wadleigh and Magistad, 1943 ; Hunter, Kelly and Somers, 1950 ; Kenworthy, 1949 ; and Taylor, 1952), and electrical resistance blocks (Hunter *et al.*, 1950 ; Schleusener, Peikert and Carolus, 1949 ; and Taylor, 1952) to determine the " critical dry point " prior to watering. In some experiments a calculated amount of water has been applied at each irrigation, to re-wet the soil to field capacity (Ayers *et al.*, 1943 ; and Hunter *et al.*, 1950), but the method has generally involved weighing plants in containers and so is inapplicable in the open ground.

In the present investigations, different, definable and reproducible water-regimes were maintained by using instruments buried in the soil to indicate the chosen " critical dry points " and at each irrigation applying calculated amounts of water to return the block of soil to field capacity.

Little work appears to have been done on the effects of specific water-regimes on the growth of the tomato (*Lycopersicum esculentum* Mill.) under glasshouse conditions, and these investigations were designed to find the effects of different water-regimes on the root development, growth and yield of tomatoes under glass.

EXPERIMENTAL METHODS.

The plots.

A vinery type glasshouse was subdivided into twenty-four plots by water-proofed brick walls which penetrated the subsoil. Each plot was approximately 210 cm.×

180 cm. and contained a bed of about 20 cm. of coarse sandy loam top-soil overlying about 40 cm. of slightly heavier, well-drained, cultivated subsoil resting on massive, well-structured but undisturbed Keuper marl. The layout of the plots enabled four treatments to be replicated six times in randomized plots to minimize the marked positional effects which are found under glass. (See Fig. 4.)

Instruments.

Soil moisture tensiometers seemed likely to provide the best method of measuring soil moisture at the relatively low tensions contemplated for this experiment. Three types of tensiometer were used, viz. Rogers' vacuum gauge model (Rogers, 1936), Rogers' manometer model (Rogers, 1935), and a commercial model.

Plaster of Paris electrical resistance blocks made to Wolfe's specifications (1951) were also used to assess soil moisture in order to determine their range of sensitivity and for comparative purposes, but were not used for irrigation control.

Recording thermographs, thermometers, hygrometers and Piche evaporimeters were used to measure the glasshouse climate, but irrigation control was not based on any of these records.

Methods.

For the purpose of this experiment a water-regime was defined as a system of irrigation in which the soil moisture is allowed to fluctuate only between field capacity and a predetermined level of dryness, as indicated by the moisture tension measured at 15 cm. below the surface (Hudson and Salter, 1953). The tensions, chosen arbitrarily, at which it was decided to apply water were 7, 15, 30 and 60 cm. of mercury for the four treatments respectively. Under the conditions of this experiment these tensions indicated that approximately 5, 35, 50 and 60 per cent. respectively of the available soil moisture had been removed from the soil from the vicinity of the tensiometer pots.

Cultural details.

Seed of two varieties, Ailsa Craig and Single Cross, were sown on 24th January 1952, and the seedlings were pricked off on 9th February into pots. Early in March the plots were thoroughly flooded with water, allowed to drain and given a normal commercial dressing of base fertilizer. Planting took place on 31st March, and " ball-watering " was carried out from this time until 25th April, by which time the plants had well-developed root systems. (" Ball-watering " is the term used to describe the application of small quantities of water to the soil immediately around the base of each young plant.) The soil in each plot was then wetted to field capacity. The differential watering treatments started from this date and continued until root sampling had been completed in November.

Apart from watering, the plants were treated normally throughout the season. All plots received the same total amount of nutrient, which was applied in solid form prior to watering and washed in.

Plot layout.

Ten uniform plants of each variety were planted in each plot, the varieties being separated from each other by a central path 25 inches wide. The planting distance of 15 inches × 15 inches was closer than normal commercial spacing and represented

a total plant population of 20,000 per acre, excluding the space taken by the main pathway in the centre of the glasshouse.

Irrigation control.

One plot, chosen at random, was used to control the watering throughout the season of all the plots in that treatment, i.e. all six plots were watered when the soil moisture tensiometer in the key plot recorded the pre-determined reading. It had already been found that much of the root system of the tomato plant grown under glass was located in the top 30 cm. of soil with the main concentration of roots between 5 and 25 cm. deep. The tensiometer pots to be used for irrigation control were therefore placed at a depth of 15 cm. well away from the wall and the path. Tensiometers were also installed with their pots at a depth of 45 cm. but these were not used in connection with irrigation control. Readings were taken daily at 0900 hours to minimize the effect of diurnal fluctuations. (Haise and Kelley, 1950 ; and Richards and Neal, 1936.)

Calculations of water requirement.

Every two or three weeks, the approximate water deficit of each key plot at the " critical dry point " was assessed by a rough calculation based on (*a*) the soil moisture characteristic curve, (*b*) the estimated amount of water required to increase the moisture content of a unit volume of this particular soil by 1 per cent., and (*c*) the volume of soil which required to be re-wetted, estimated by using a Veihmeyer tube to ascertain the depth to which the soil was strongly ramified by roots and multiplying that depth by the area of the plot. In fact, of course, moisture is not withdrawn from various levels of the soil at a uniform rate and water deficits calculated in this way can only be approximate, but they probably gave a useful guide to the amount of water required at each irrigation to replace that which had been lost since the previous one.

On each occasion when a plot was watered, sufficient water was applied to make good the calculated water deficit, thus rewetting the whole bed of soil approximately to field capacity.

The volume of water applied per plot at each watering naturally varied at different times and from treatment to treatment, ranging from as little as 14 litres per plot in the wettest treatment early in the season, when most of the roots were confined to a relatively shallow layer of soil, to as much as 318 litres per plot in the driest plots towards the end of the season when the tomato roots had ramified through the whole bed of soil. Similarly, frequency of application of water varied widely, from almost daily watering of the wettest plots to approximately monthly applications to the driest plots.

Growth measurements.

Detailed measurements of growth and yields were made on six plants of each variety from each plot, at monthly intervals, i.e. 36 plants for each variety and each treatment.

As a measure of the vegetative growth of the aerial part of the plants, the method of Ross (1946) was used to combine the height of the plant and its mean diameter by means of regression equations, to give the calculated dry weight of the vegetative aerial parts of the plant. The regression equation for each variety, obtained in a separate experiment, was as follows :

Ailsa Craig .. $y=0{\cdot}3886x-5{\cdot}74$ $r=+0{\cdot}97$ $P=<0{\cdot}01$
Single Cross .. $y=0{\cdot}3826x-4{\cdot}85$ $r=+0{\cdot}987$ $P=<0{\cdot}01$
where x=Height (cm.) × mean diameter (cm.)^2
and y=Dry weight (gm.) of the vegetative parts of the plant.
r=Correlation coefficient.

Root studies.

In addition to the root sampling made for irrigation control, more detailed studies were made of root distribution half way through the growing season and at the end of the experiment. Borings were made to a depth of 60 cm. at four sites 10 cm., and four sites 15 cm. from the base of plants in a set pattern. For the June sampling, four plants were selected at random for each variety and from each treatment. At the end of the season twelve plants were sampled from each treatment and for each variety. Successive 10 cm. cores were removed from the borings, washed on a 1 mm. sieve and the roots divided into two grades, i.e. greater and less than 1 mm. in diameter respectively. The total length and number of roots in each grade were recorded.

At the end of the season a profile mapping method was also used for comparison with the sampling technique. Trenches were dug, 1 metre deep and 15 cm. from the bases of plants, and the exposed root ends plotted as they appeared on the vertical faces. This method was applied to two plants for each variety in each treatment.

Soil analysis.

At the end of the season soil samples were taken from each plot at depths of 0–8 cm. and 15–23 cm. The samples were analysed for organic matter, total nitrogen, phosphorus, potassium and magnesium. In addition pore space, pH and pC figures were obtained.

EXPERIMENTAL RESULTS.

TABLE I.

Irrigation particulars and mean yields per plant from 25th April to 4th October, 1952 (inclusive).

Treatment	Irrigation data			Average yield per plant*			
	Tension at which water applied (cm. Hg)	Number of times water applied	Total amount of water applied (litres/plant)	Ripe fruit		Total yield (incl. green fruit picked 4th October)	
				Ailsa Craig (kgm.)	Single Cross (kgm.)	Ailsa Craig (kgm.)	Single Cross (kgm.)
A (Wet) ..	7	136	124·6	3·4	2·6	†4·2	3·2
B	15	17	88·6	3·2	2·2	3·8	2·6
C	30	9	75·0	3·1	2·2	3·5	2·5
D (Dry) ..	60	5	72·7	2·6	1·8	3·0	2·1

* Average of sixty plants for each variety in each treatment.

† Equivalent to a yield of 86 tons per acre at the spacing of plants in the experiment, excluding the space taken by the path down the centre of the house.

The brackets indicate that the differences are not significant (i.e. $P>0{\cdot}05$).

TABLE II.

Percentages of each grade of ripe fruit produced per treatment.

Variety	Grade*	Treatments			
		A (Wet)	B	C	D (Dry)
		%	%	%	%
Ailsa Craig	Pink (5–8 to the lb.)	8·1	9·5	6·6	4·0
	Pink and white (8–12 to the lb.) ..	63·6	53·6	54·6	45·4
	White (11–16 to the lb.)	26·7	35·2	36·7	47·7
	Chat (more than 16 to the lb.) ..	1·6	1·7	2·1	2·9
Single Cross	Pink	20·8	19·4	16·6	13·2
	Pink and white	63·8	60·5	58·7	55·2
	White	14·8	19·4	23·3	30·0
	Chat	0·6	0·7	1·4	1·6

* Graded to the specifications of the Ministry of Agriculture's National " Recommended " Grade Scheme. The " Pink and White " grade is usually regarded as the most desirable in commercial practice.

Yields of fruit.

Table I gives the average yield of fruit per plant under the four treatments, showing that yields were progressively reduced as the soil moisture tension rose before watering. Under all treatments Ailsa Craig produced more fruit than Single Cross.

Grades of fruit.

The grade of fruit was affected by the treatments, as shown in Table II. The average size (weight) of each fruit was progressively smaller under the drier regimes.

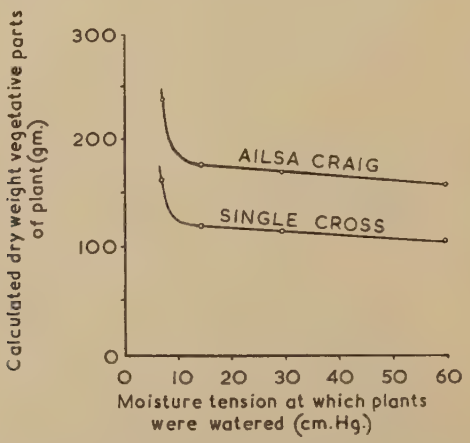

FIG. 1.

Relationship between calculated dry weights of vegetative parts of the plants, and moisture tensions at which they were watered. (Mean of 18 plants.)

EFFECT OF TREATMENTS ON VEGETATIVE GROWTH OF TOMATO PLANTS.

Shoot development.

By July, plants growing under the wettest conditions (treatment A) were larger and more vigorous than plants growing under the drier regimes.

At the end of the experiment (October) the height and mean diameter of stems were again recorded and were combined by means of the regression equations to give the calculated dry weights illustrated in Fig. 1. The differences between treatments A and B for both varieties are significant (P=0·01) but other differences are not. Thus vegetative growth was markedly affected by the drier soil moisture regimes. Ailsa Craig was always more vigorous than Single Cross.

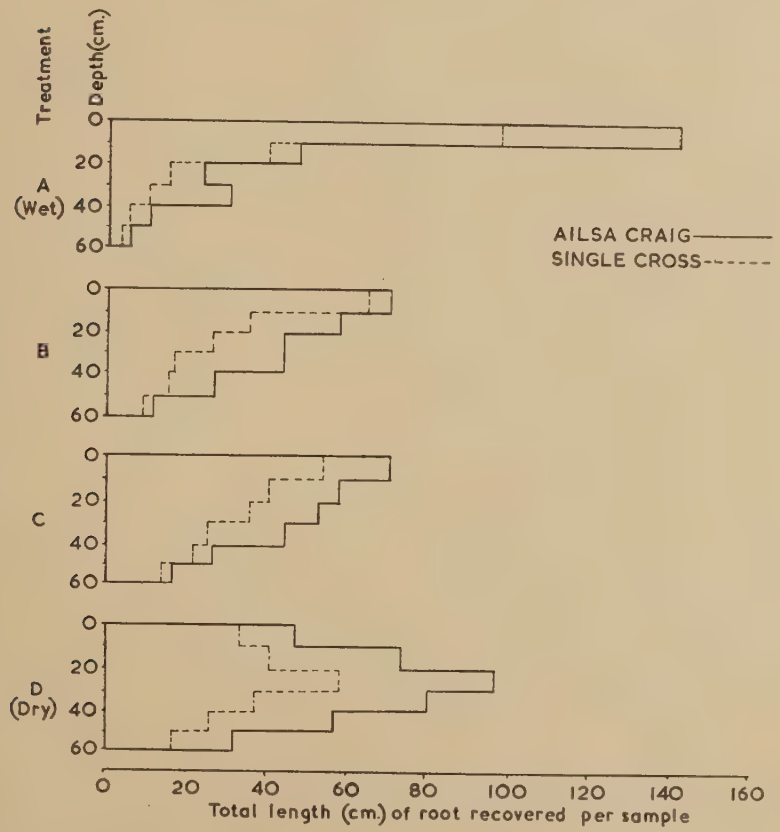

FIG. 2.

Amount of root (less than 1 mm. diam.) removed by sampling in June, showing depth distribution. (Each the mean of 4 plants.)

Diseases.

Normal measures prevented Tomato Leaf Mould (*Cladosporium fulvum* Cooke) from becoming serious on any of the tomato plants. Very few plants were attacked by Grey Mould (*Botrytis cinerea* Pers. ex. Fr.).

Root development.

June sampling. The distribution in depth of roots less than 1 mm. in diameter is shown in Fig. 2. There was a progressive increase in the amount of root at the lower depths under the drier treatments.

October sampling. The distribution in depth of roots less than 1 mm. in diameter in October is shown in Fig. 3. Although the relative distribution was similar to that obtained in June, the maximum root zone for both varieties under treatment C was rather deeper than in June.

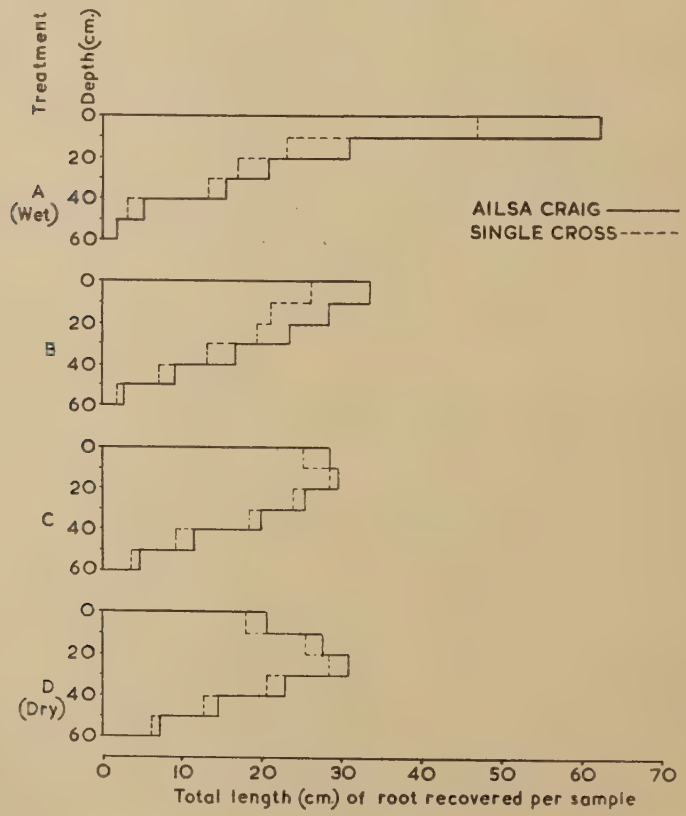

FIG. 3.

Amount of root (less than 1 mm. diam.) removed by sampling in October, showing depth distribution. (Each the mean of 4 plants.)

It is of interest to note that at each sampling both varieties had responded similarly to the four water-regimes, although Ailsa Craig always had more roots than Single Cross.

The vertical distribution of roots as shown by the profile mapping method agreed closely with that obtained from sampling.

Effects of water-regimes on soil analyses.

Prior to construction of the plots the whole glasshouse had been cropped uniformly for 5 years. In preparing the plots the soil was standardized as far as possible. Chemical analysis showed that at the outset of the experiment the soil in all plots was reasonably uniform and showed no marked trends between differently treated plots.

Table III.

Chemical analysis of the soil at the end of the experiment. Depth 0–3 inches. (Mean of 6 determinations.)

	Treatments			
	A (Wet)	B	C	D (Dry)
% Organic matter	3·41	3·31	3·10	3·02
pH	5·9	5·8	5·7	5·7
pC	3·81	3·51	3·43	3·28
% Total nitrogen	0·170	0·185	0·205	0·191
% Citric soluble phosphate	0·060	0·068	0·072	0·073
Potassium p.p.m. extracted in N. ammonium nitrate sol.	46·5	54·7	74·2	82·5
Magnesium p.p.m. extracted in N. ammonium nitrate sol.	21·2	23·3	25·8	25·2
Depth 6–9 inches pC	3·57	3·64	3·47	3·50

Analyses at the end of the experiment indicated strong treatment effects as follows : (*a*) The amount of citric soluble phosphate and exchangeable potassium remaining in the surface layers of soil was progressively greater from treatments A (wet) to D (dry). (*b*) A similar trend showed for total nitrogen and exchangeable magnesium. (*c*) A progressive increase in the concentration of remaining soluble salts (as reflected by pC figures) was shown from treatments A to D. (*d*) A progressive reduction in organic matter remaining in the soil from treatments A to D.

DISCUSSION.

The principle of subjecting plants to definable water-regimes is not new but, as far as has been ascertained, this approach has not been used previously to determine the effects of different water-regimes on the tomato plant under glasshouse conditions. The use of an instrument buried in the soil, to give an indication of soil moisture in its immediate vicinity, together with the application of calculated amounts of water to make good the water deficits at each watering, represents a higher standard of

irrigation control than is normally found under glasshouse conditions when empirical methods are used to determine the timing and amount of irrigation.

The total amount of water applied to each treatment over the five months is given in Table I, but caution is necessary when comparing total amounts of water in this way. For example, the difference between the total quantity of water applied to treatments C and D over the entire season amounts to only 2·3 litres per plant, but the different frequencies of watering, e.g. at 30 cm. and 60 cm. tensions respectively, resulted in significant differences in average yield from the plants under the two treatments.

There was little correlation between the resistances of the plaster of Paris blocks and the soil moisture percentage under the conditions of this experiment, i.e. at the wetter end of the available moisture range, findings which agree with those of several other workers.

Under the conditions of this experiment, the yield and size of fruit from the tomato plant were greatly influenced by soil moisture conditions over a comparatively wide range. In contrast, Veihmeyer and Hendrickson's experimental work on fruit trees in the United States led them to assert (1950) that " The fact that trees can obtain a supply of water from the soil with equal facility between the field capacity and the permanent wilting percentage, and that size and quality will not be affected adversely unless the moisture content is reduced to the permanent wilting percentage, points the way for efficient use of water in orchard irrigation."

The responses to moisture tension found in the present work may be connected with the very different habits of growth of the tomato plant as compared with deciduous fruit trees. It is generally accepted that plants need most water when they are growing strongly. It is, therefore, not surprising to find that the heaviest yields of tomatoes under glass were produced under the water-regime that maintained the plant in the most active vegetative growth, since the tomato plant must continue to grow until late in the season if it is to crop heavily.

Fig. 1 shows that more *growth* (as reflected by calculated dry weight) was made under the lowest moisture tension conditions than where higher tensions developed, whereas little difference in vegetative growth was found between the 15 and 60 cm. regimes. Comparison of this result with the relationship between *yield* and tension suggests that the greatly increased vegetative growth made under the low tensions was not accompanied by a proportional increase in yield, even though for Single Cross there was a significant difference in average yield between treatments A and B.

The effects of the different water-regimes on the root development of the tomato plants is of considerable interest. Distribution of the roots was markedly affected, the zone of greatest root development being in the 0–10 cm. soil layer under the wettest treatment and in the 20–30 cm. layer under the driest treatment. The vertical distribution of roots less than 1 mm. in diameter was markedly similar for both varieties although proportionately more roots were found at all depths for Ailsa Craig than for Single Cross.

Russell (1950) has suggested that plants usually have a shallow root system when grown in moist fertile soils because the aerial parts consume most of the carbohydrates produced by the plant. Conversely, a drought after the plant has become established encourages a deep rooting system, since the first effect of water shortage in the soil is to reduce the rate of new aerial growth and hence more carbohydrate is made available for root growth. Salisbury (1937), however, suggests that the

PLATE I

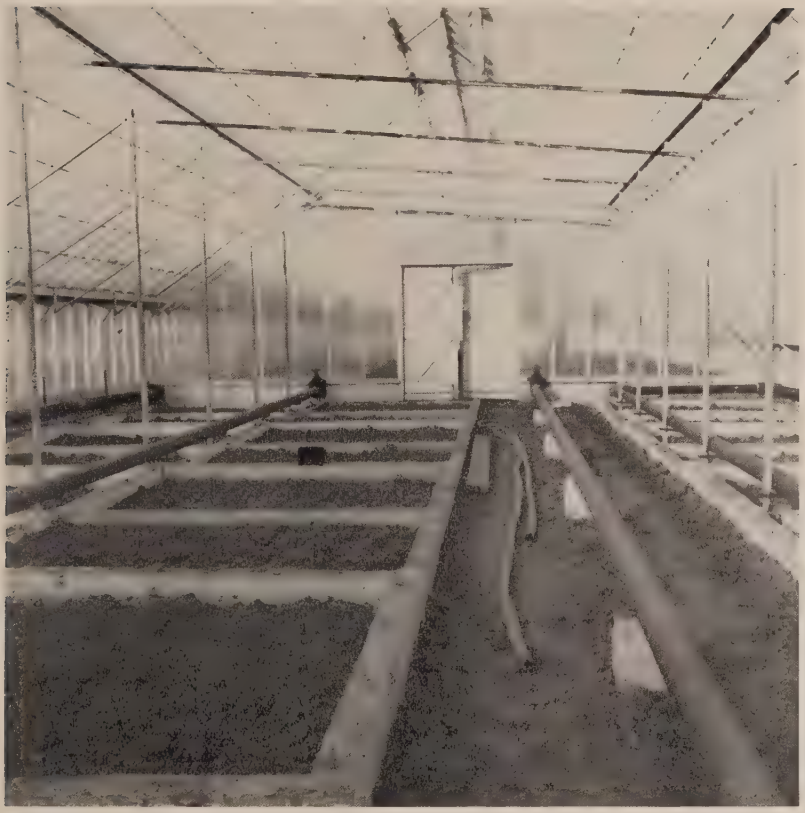

Fig. 4
Lay-out of part of glasshouse, showing brick lined plots used for maintaining different water-regimes. The walls are capped with slabs, used as paths, to avoid walking on beds.

[face page 266

reduction in root development in wet soils is mainly due to deficient aeration.

Different water-regimes markedly affected the chemical composition of the soil. The organic content appeared to disappear more rapidly under drier treatments, possibly owing to increased rate of oxidation under conditions of better aeration.

The pC figures show a reduction in the concentration of soluble salt at a depth of 0-3 inches in the wet treatment. Citric soluble phosphate, exchangeable potassium, and to a lesser extent total nitrogen and exchangeable magnesium appear to have been affected by the treatments, but further work is needed to elucidate this aspect.

In a similar experiment in 1953, tomatoes again grew best under conditions of low moisture tension whilst plants made less vegetative growth and yielded less fruit in treatments where relatively high tensions were allowed to develop before watering, even though the driest condition of the soil never approached the permanent wilting point. The 1953 results also confirmed that the system of applying water (i.e. the water-regime) might have more effect on growth and yield than has the total amount of water applied.

SUMMARY.

An investigation was made to find the effect of different water-regimes on the root development, growth and yield of the tomato under glasshouse conditions.

The concept of the water-regime is explained and a description given of the instruments, apparatus and experimental procedure adopted, which enabled plants of two varieties of tomato to be subjected to four different, definable and reproducible water-regimes for a continuous period of five months. In the different regimes, water was not applied until 5, 35, 50 and 60 per cent. respectively of the available water had been removed from the soil at a depth of 15 cm., as indicated by soil moisture tensiometers. The timing of irrigation was thus controlled by tensiometer readings.

Growth and yield of tomatoes were markedly affected by the water-regimes, maximum growth and yield being produced when the soil moisture content was maintained in the region of field capacity and progressively reduced in drier treatments. Root development, determined by sampling and examination of soil profile, was also affected, the zones of greatest concentration of roots being located at different depths under the different water-regimes. Chemical composition of the soil was also affected.

ACKNOWLEDGMENTS.

I am greatly indebted to Mr. J. P. Hudson for encouragement, interest and advice given during this work, which was carried out under his supervision, in the Department of Horticulture. Grateful acknowledgment is also made of the interest, help and advice on matters of soil chemistry given by Mr. D. V. Crawford of the Department of Agricultural Sciences.

Grateful acknowledgment is made of a grant from the Agricultural Research Council which has met the cost of this work from July, 1953.

REFERENCES.

Ayers, A. D., Wadleigh, C. H., and *Magistad, O. C.* (1943). The interrelationships of salt concentration and soil moisture content with the growth of beans. J. Amer. Soc. Agron., **35,** 796.

Haise, H. R., and *Kelley, O. J.* (1950). Causes of diurnal fluctuations of tensiometers. Soil Sci., **70,** 301.

Hudson, J. P., and *Salter, P. J.* (1953). Effects of different water-regimes on the growth of tomatoes under glass. Nature, Lond., **171,** 480.

Hunter, A. S., Kelly, W. C., and *Somers, G. F.* (1950). Effects of variations in soil moisture tension upon the ascorbic acid and carotene content of turnip greens. Agron. J., **42,** 96.

Kenworthy, A. L. (1949). Soil moisture and growth of apple trees. Proc. Amer. Soc. hort. Sci., **54,** 29.

Richards, L. A., and *Neal, O. R.* (1936). Some field observations with tensiometers. Proc. Soil Sci. Soc. Amer., **1,** 71.

Rogers, W. S. (1935). A soil moisture meter depending on the capillary pull of the soil. J. agric. Sci., **25,** 326.

——— (1936). The relation of soil moisture to plant growth, illustrated by moisture meter experiments with strawberries. Rep. E. Malling Res. Sta. for 1935, 111.

Ross, A. A. (1946). Studies of growth correlations in the tomato. Qd. J. agric. Sci., **3,** 121.

Russell, E. J. (1950). Soil Conditions and Plant Growth. 8th Ed. London: Longmans, Green.

Salisbury, E. J. (1937). The plant and its water supply. J. R. hort. Soc., **62,** 425.

Schleusener, P. E., Peikert, F. W., and *Carolus, R. L.* (1949). Results of irrigation on vegetable crops. Quart. Bull. Mich. agric. Exp. Sta., **31,** 343.

Shantz, H. L. (1927). Drought resistance and soil moisture. Ecology, **8,** 145.

Taylor, S. A. (1952). Use of mean soil moisture tension to evaluate the effect of soil moisture on crop yields. Soil Sci., **74,** 217.

Veihmeyer, F. J. (1927). Some factors affecting the irrigation requirements of deciduous orchards. Hilgardia, **2,** 125.

——— and *Hendrickson, A. H.* (1950). Responses of fruit trees and vines to soil moisture. Proc. Amer. Soc. hort. Sci., **55,** 11.

Wolfe, J. S. (1951). Plaster of Paris blocks for soil moisture measurement. Grower, **36,** 423.

(*Received* 14/1/54.)

EFFECTS OF FRUIT THINNING BY THE LEAF COUNT METHOD ON YIELD, SIZE AND BIENNIAL BEARING OF THE APPLE DUCHESS FAVOURITE

By A. P. PRESTON
East Malling Research Station

THOUGH much research has been done on thinning apples in the U.S.A. (see Gourley and Howlett, 1941) little has been done in England. In 1945 it was decided to test the effects of early and late thinning, at various intensities, upon some mature apple trees at East Malling. To obtain precise information, the trees were thinned by the leaf-count method (Magness, Overley and Luce, 1931) in preference to the more familiar spacing method.

MATERIALS AND METHODS.

Fourteen-year-old spur-pruned trees of Duchess Favourite on M.IX forming double buffer rows to a manurial trial were available for the experiment. Trees were selected from adjoining plots that received both nitrogen and potash dressings annually ; half received low potash (K) at 2 cwt. per acre sulphate of potash and the other half high potash (2K) at twice that amount (Hoblyn, 1941).

Three degrees of fruit thinning were applied at two times, early and late. To facilitate the analysis of the results, control trees were left at each time of thinning. The thinning treatments were :

10 E (or L)=1 fruit to 10 leaves, early (or late) thinned.
20 E (or L)=1 ,, ,, 20 ,, ,, ,, ,,
30 E (or L)=1 ,, ,, 30 ,, ,, ,, ,,
C E (or L)=control, unthinned, tree.

The leaves were counted on each tree and the number of fruits to be left ascertained ; the fruit was then thinned so that those remaining were evenly distributed along the branches. The early thinning was carried out from 30 to 35 days with a mean of 31 days after full bloom (50 per cent. blossoms open) and the fruitlets removed averaged 1·5 cm. in diameter. Late thinning was carried out immediately after the June drop had been recorded and varied with the season from 64 to 93 days with a mean of 74 days after full bloom, and the fruitlets removed averaged 3·5 cm. in diameter. Fruit from trees under all treatments was picked at one time, which again varied with the season from 105 to 122 days with a mean of 113 days after full bloom.

Thinning was done by hand ; very small primary spur leaves and the immature leaves at the apices of shoots were excluded from the leaf-count. In thinning, care was taken to leave the best placed fruit, as is customary in normal orchard practice. In some years, however, insufficient fruitlets had set to enable the required ratio of fruits to leaves to be left ; this occurred mainly in " off " years, and the late-thinned trees and those that were lightly thinned were most affected. The number of trees so affected and the treatments concerned are summarized in Table I.

TABLE I.

Number of trees where thinning treatments could not be completed (8 trees per treatment).

Thinning treatment	1945	1946	1947	1948	1949	1950	1951	Total number of occasions (maximum 56)
10 E	0	1	1	6	5	6	0	19
20 E	0	0	0	0	0	2	0	2
30 E	0	0	0	0	0	0	0	0
10 L	0	7	0	8	8	8	0	31
20 L	0	0	0	0	3	7	0	10
30 L	0	0	0	1	1	5	0	7

The trees blossomed but failed to set a crop in 1944 owing to late spring frost. This caused a heavy " on " year in 1945, when the thinning treatments were first applied ; no serious late spring frosts have affected the trial since.

EXPERIMENTAL RESULTS.

Leaf area.

The leaf area of sample spurs was measured at each of the two times of thinning in 1951. On each tree four spurs were selected, one midway along each of four branches, these being situated at the four cardinal points of the tree. All leaves on each spur were measured, excluding the very small primary leaves of 1 cm. or less in diameter. The mean leaf area was 12·38 sq. cm. There was no significant difference due either to thinning treatment or manuring. Individual fruits were thus estimated as having an attendant average leaf area of 123, 247 or 371 sq. cm. respectively for the three degrees of thinning, though some of this leaf area was associated with non-bearing spurs and shoot growth.

Vigour.

The six years' measurements of shoot growth and trunk girth increment were grouped into successive two-year periods, the data being transformed to logarithms for analysis (Pearce, 1943). Neither degree nor time of thinning had any significant effect upon either shoot growth or trunk girth increment.

Fruit buds.

Fruit buds were recorded annually after pruning and factor " I " (Hoblyn *et al.*, 1936) has been calculated (Table II). This measures the intensity of fluctuation in bearing and is arrived at by dividing the difference between consecutive pairs of years by their sum, 0 denoting equal numbers of fruit buds formed, and 100 no fruit buds formed in alternate years.

The two higher degrees of thinning, 1 fruit to 20 or 30 leaves, significantly reduced the intensity of the biennial habit. The lowest degree of thinning, 1 fruit to 10 leaves, showed no improvement over the control treatment. Early thinning significantly reduced the biennial intensity.

Fruit set.

Over a five-year period, thinning 1 fruit to 20 leaves gave the best set of fruit ; the numbers of fruits set for the three degrees of thinning are summarized in Table III.

TABLE II.

Intensity of fluctuation (I) in number of fruit buds, 1945-51.

Degree of thinning ..	30	20	10	C	Sig. diff. (P=0·05)
Mean " I " ..	14	17	28	33	6
Time of thinning ..	early		late		
Mean " I " ..	12		27		5

TABLE III.

Average " fruit set " as estimated for the years 1946–49 and 1951.

Degree of thinning	C	10	30	20	Sig. diff. (P=0·05)
Mean number of fruits set per 100 blossom clusters	46·9	56·1	59·8	65·7	6·8

Incidence of June drop.

June drop was recorded from 1946. In some years unthinned trees and those thinned to 1 fruit to 10 leaves carried light crops in " off " years and the June drop in these years was negligible. In other years, when the drop was appreciable, it was estimated by expressing the number of fruitlets that had dropped between the times of early and late thinning as a percentage of those remaining on the trees after early thinning. In Table IV the drop from the unthinned (C) trees is compared with that from trees receiving the three degrees of early thinning. The loss of fruit from June drop, after early thinning, is very small indeed except on trees that were lightly thinned in 1949.

TABLE IV.

Mean percentage June drop.

	Degrees of early thinning			
Year	30	20	10	C
1947	4·6	3·0	3·5	11·4
1949	8·0	11·0	28·1	25·5
1951	10·6	9·3	13·4	26·4

Differences that are not significant (P>0.05) are indicated by brackets.

Fruit yield.

The average effect of degree of thinning at both times on annual fruit yield is shown in Fig. 1. The late spring frost, in 1944, put all trees into a heavy " on " year

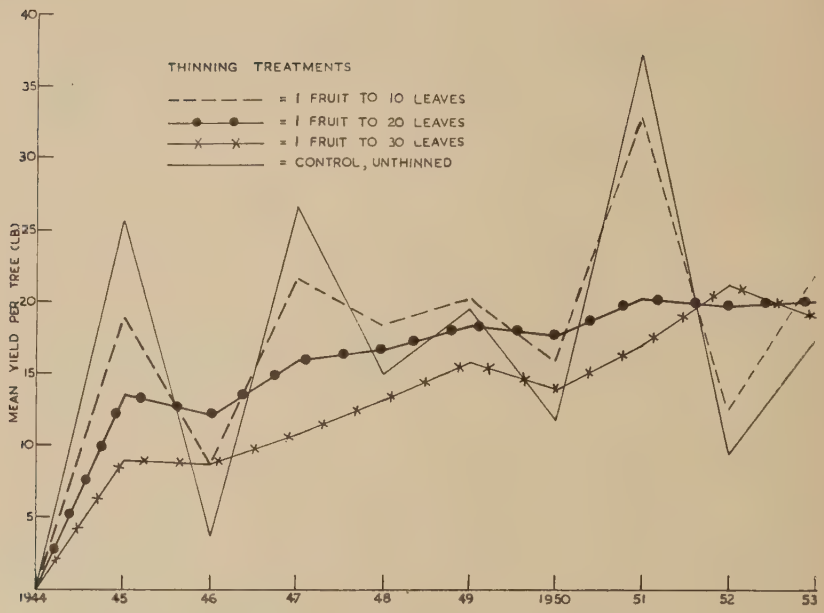

FIG. 1.
Effect of degree of thinning on fruit yield. No thinning treatments were applied to the trees in either 1952 or 1953.

in 1945 which began a biennial rhythm. This persisted markedly in trees thinned to 1 fruit to 10 leaves as well as in unthinned trees until 1948, when the fluctuation lessened. A heavy set of fruit in 1951, however, renewed the intensity of the biennial habit.

TABLE V.

Effect of degree of thinning on fruit yield in lb. per tree.

Year	Degree of thinning				Sig. diff. (P=0·05)
	C	10	20	30	
1945	25·6	18·9	13·4	9·0	3·9
1946	3·7	8·7	12·0	8·7	2·8
1947	26·6	21·6	15·9	10·8	5·5
1948	15·0	18·3	16·7	13·2	n/s
1949	19·5	20·2	18·4	15·9	n/s
1950	11·8	15·9	17·7	14·0	n/s
1951	37·2	32·9	20·3	17·0	6·9
Totals	139·4	136·5	114·4	88·6	

The yield from trees under the lightest thinning treatment, 1 fruit to 10 leaves, was much the same as that on the unthinned trees; trees undergoing more drastic degrees of thinning, 1 fruit to 20 or 30 leaves, carried, on the whole, smaller but useful crops each year with a marked tendency towards an annual increase in yield. The difference was highly significant in four out of seven years (Table V); times of thinning differed significantly in two years only (1946 and 1948), in opposite directions each year, and cannot be regarded as having had a marked influence on fruit yield.

The intensity of the biennial habit (I) was evaluated from the total number of fruits harvested. Table VI shows that all degrees of thinning produced more regular cropping trees than the controls. However, while there was no difference in regularity in the early thinned trees, where the trees were thinned late the more heavily thinned trees were more regular. It is noteworthy that this differential effect of time and degree of thinning did not appear in the fruit buds (Table II) in which the higher degrees were better, irrespective of time of thinning.

TABLE VI.

Intensity of fluctuation (I) in number of fruits, 1945-51.

	Time of thinning	Degree of thinning				Sig. diff. (P=0·05)
		30	20	10	C	
Mean " I "		20	17	29	50	9
Interaction (Time × Degree)	Early	20	20	18		n/s
	Late	19	15	40		13·

Fruit size and quality.

Measurements of fruit size showed that unthinned trees carried smaller fruits than those under the higher degrees of thinning, and this difference was most pronounced during years of heavy yield (Table VII). Crops of relatively large fruits were carried by the unthinned trees during their " off " years, and these did not differ for fruit size from those of the thinned trees. Although the fruit yield from thinned and unthinned trees did not differ significantly in 1949 (Table V), a year of severe

TABLE VII.

Fruit size. Mean weight of 100 fruits (lb.).

Year	Fruit yield (lb.) for control trees	Degree of thinning				Sig. diff. (P=0·05)
		C	10	20	30	
1945	25·6	10·8	17·0	19·5	20·1	1·8
1946	3·7	19·0	16·8	17·1	19·6	n/s
1947	26·6	14·3	16·0	19·1	20·5	1·1
1948	15·0	17·3	15·7	18·1	19·2	2·4
1949	19·5	10·9	11·2	12·1	13·7	0·9
1950	11·8	16·3	16·1	17·6	18·4	1·2
1951	37·2	10·3	11·3	14·4	15·3	1·0

summer drought, those under the higher degrees of thinning yielded larger fruits than the unthinned trees. Time of fruit thinning had little effect on fruit size; early thinned trees gave larger fruits than late thinned ones in only two years out of seven (1945 and 1947).

In 1951, a severe outbreak of Fruit Tree Red Spider Mite (*Metatetranychus ulmi* Koch) occurred on some of the experimental plots during July and August. All trees were scored for affected foliage and the data were analysed. A negative correlation, which was significant ($P<0.05$ and little more than 0·01), showed that the greater the red spider damage the smaller the fruits at harvest. On plots having an average infestation two-thirds greater than on others, the mean fruit size was reduced by about 6 per cent.

Two criteria were used to assess possible treatment differences in early ripening of the fruit. Firstly, the percentage of dropped fruits immediately before picking, as this might indicate early ripening with an early maturing variety such as Duchess Favourite. Secondly, the ground colour on the harvested fruit, which varied from green to yellow and was recorded by a visual method in five categories for each tree in which category 1=green and category 5=yellow. Data for the first of these two criteria have shown inconsistent differences for the effect of degree of thinning throughout the trial. Only in one year, 1947, was there a significant effect of time of thinning, when early thinned trees had more dropped fruits than late thinned ones.

Ground colour, however, has shown a marked effect of degree of thinning ; trees under the higher degrees, 1 fruit to 20 or 30 leaves, yielded yellower fruits than those which were lightly thinned or unthinned, and in this trial this factor appears to be a more reliable guide to early maturity than the percentage of pre-harvest dropped fruit. Even very lightly thinned trees, 1 fruit to 10 leaves, gave fruits that were yellower than those from unthinned trees (Table VIII).

TABLE VIII.

Fruit colour. Mean categories for amount of red colour and ground colour, 1945-51.

	Degree of thinning				Sig. diff. (P=0·05)
	C	10	20	30	
Red colour	2·4	2·5	3·1	3·1	0·3
Ground colour	2·2	2·5	3·1	3·0	0·2

The amount of red colour on harvested fruits was also recorded visually in five categories. The data are summarized in Table VIII, the higher values indicating more colour. Throughout the trial trees under the higher degrees of thinning gave fruits that were redder than those from trees that were lightly thinned or unthinned.

Manurial interaction.

High and low potash (K and 2K) treatments on the experimental plots affected several factors in the thinning trial. On the plots with higher potash, the late

thinned trees were less regular than the early thinned ones in fruit bud formation, the mean intensity of fluctuation (I) was :

Early ..	3	Late ..	14	($P<0.05$)

Over the five years 1946-49 and 1951, estimated fruit set was increased in late thinned trees but reduced in early thinned ones on the plots receiving higher potash. The difference between early and late thinning treatments at the two levels of potash was :

Early-late (K)	5·5	($P<0.05$)
Late-early (2K)	9·0	

These manurial interactions will be discussed later.

Residual effect of thinning treatments.

Thinning treatments were applied for the last time in 1951, but yield and fruit size were recorded from the experimental trees in 1952 and 1953. A residual effect of degree of thinning was recorded for fruit yield in 1952 :

					Sig. diff. ($P=0.05$)
Degree of thinning ..	C	10	20	30	
Fruit yield (lb.) ..	9·4	12·4	19·8	21·2	4·9

Residual thinning treatment differences for fruit yield in 1953 were not significant but there was no reduction in yield from the trees thinned to either 1 fruit to 20 leaves or 1 fruit to 30 leaves during the previous seven years (Fig. 1).

No significant residual effects of either time or degree of thinning were recorded for fruit size on the experimental trees for either 1952 or 1953.

DISCUSSION.

In this work the most important effect of time of thinning on Duchess Favourite on M.IX has been to influence regularity in fruit bud formation ; early thinning significantly reduced the intensity of the biennial habit compared with late thinning. Furthermore, the loss of fruit after early thinning, by June drop, was very small and does not warrant delaying the thinning operation until the June drop is finished.

Degree of thinning influenced many factors. Trees under the lightest degree of thinning, that of 1 fruit to 10 leaves, showed little improvement in regularity of fruit bud formation, fruit yield or fruit size over those that were unthinned. The higher degrees of thinning, however, that of 1 fruit to either 20 or 30 leaves, gave trees that were more regular both in the number of fruit buds and the fruits harvested ; there was also a higher fruit set. Thinning 1 fruit to 30 leaves, however, depressed the crop severely in some seasons, and this was not compensated for by any significant increase in either regularity of bearing or fruit quality when compared with thinning 1 fruit to 20 leaves. Fruit size and quality were better on both the heavily thinned treatments, but thinning 1 fruit to 20 leaves gave the most valuable crops over the whole period. These results are, of course, based on a single variety on a dwarfing rootstock. It is highly probable that different ratios of fruits to leaves may be required by other varieties of apple, especially where the intensity of the biennial habit is high.

An increase in potash application increased the fruit set in late thinned trees ; they therefore carried more fruits much later in the season and at a critical time for fruit bud formation than did the early thinned trees. This doubtless caused the significant increase in biennial intensity in fruit bud formation recorded for these trees. It seems, therefore, that where potash manuring was high the trees benefited from early thinning and an increase in the intensity of the biennial habit was avoided.

The residual effect of the degree of thinning on fruit yield, which reached significance in the first year after completion of the treatments, suggests that annual fruit thinning of apple trees may not be necessary. Fruit thinning to 1 fruit to either 20 or 30 leaves in a year of heavy set, as in 1951, resulted in regular crops of good-sized fruit during the following two years without further thinning.

SUMMARY.

1. Results from a fruit thinning trial on fourteen-year-old trees of Duchess Favourite on M.IX are presented. The trees were thinned at two times, early or late, and to one of three degrees, using the leaf-count method, thinning 1 fruit to either 10, 20 or 30 leaves.

2. Thinning treatments had no significant effect upon either shoot growth or trunk girth increment. Early thinning reduced the intensity of the biennial habit in fruit bud formation. The loss of fruit after early thinning, by June drop, was very small.

3. Trees thinned to 1 fruit to 10 leaves were little better than unthinned trees for regularity in fruit bud formation, fruit yield and fruit size, but the higher degrees of thinning made the trees more regular in fruit bud formation and overcame biennial bearing.

4. The cropping of trees thinned to 1 fruit to 30 leaves was depressed without any improvement in regularity of bearing or fruit quality compared with trees thinned to 1 fruit to 20 leaves, which gave the most valuable fruit over the whole period.

5. Data on Fruit Tree Red Spider Mite damage showed that the greater the damage to the leaves the smaller were the fruits at harvest.

6. A residual effect of degree of thinning on fruit yield was recorded for two seasons after cessation of the thinning treatments.

ACKNOWLEDGMENTS.

The writer gratefully acknowledges the help of the Statistical Section in planning the trial and advising on sampling methods, and in particular two recent members of that Section, Miss Joan Fuller and Mr. J. Taylor, who undertook most of the analyses of variance.

REFERENCES.

Gourley, J. H., and *Howlett, F. S.* (1941). Modern fruit production. Macmillan Co., New York.

Hoblyn, T. N., Grubb, N. H., Painter, A. C., and *Wates, B. L.* (1936). Studies in biennial bearing. J. Pomol., **14,** 39-76.

——— (1941). Manurial trials with apple trees at East Malling, 1920-39. J. Pomol., **18,** 325-43.

Magness, J. R., Overley, F. L., and *Luce, W. A.* (1931). Relation of foliage to fruit size and quality in apples and pears. Wash. agric. Exp. Sta. Bull. **249.**

Pearce, S. C. (1943). The statistical interpretation of vigour measurements of fruit trees. J. Pomol., **20,** 111-15.

(*Received* 26/1/54.)

MOLYBDENUM AS A PLANT NUTRIENT

III. THE INTERRELATIONSHIPS OF MOLYBDENUM AND NITRATE SUPPLY IN THE GROWTH AND MOLYBDENUM CONTENT OF CAULIFLOWER PLANTS GROWN IN SAND CULTURE

By S. C. AGARWALA* and E. J. HEWITT
A.R.C. Unit of Plant Nutrition (Micronutrients), Long Ashton Research Station, University of Bristol

Previous papers in this series (7, 8) have described the effects of molybdenum deficiency in several crops. Brassica crops were shown to be of especial interest because of the appearance of whiptail or related symptoms under conditions of molybdenum deficiency, to which the genus is relatively sensitive. The whiptail syndrome comprises malformation of mainly younger leaves which may produce an elongated midrib, partially or entirely devoid of lamina. Death of the stem growing point and other types of tissue breakdown are associated features. These symptoms may or may not be preceded by other symptoms of mottling, wilting and scorching of older leaves often during the earliest stages of growth (4, 6, 7). The essentiality of molybdenum in nitrate assimilation is now recognized (6, 12, 16, 20), and it was thought desirable to study in more detail the relationships of growth and whiptail and other symptoms of molybdenum deficiency to molybdenum status, nitrate assimilation and other metabolic factors, especially as previous work (7) suggested that whiptail symptoms might not always occur under the most severe molybdenum deficiency conditions. The present paper is confined mainly to effects on growth and on molybdenum status of plants given a high or low supply of nitrate nitrogen over a wide range of molybdenum levels. Changes in ascorbic acid, nitrogen and carbohydrate fractions and effects of using nitrogen sources other than nitrate will be described separately.

EXPERIMENTAL.

Materials and methods.

Sand culture.

Cauliflower plants, variety Majestic, were grown in purified sand cultures using the methods fully described elsewhere (2). Nitrogen was supplied as nitrate at two levels : 6 (N_1) or 24 (N_2) m. eq./L. as shown below.

	6 m. eq. level : N_1	24 m. eq. level : N_2
KNO_3	4 m. eq./L.	4 m. eq./L.
$Ca(NO_3)_2$	2	8
$CaSO_4$	6	nil
$NaNO_3$	nil	12

The net changes were therefore in sulphate, which was higher in the 6 m. eq./L. NO_3 (N_1) series, and in sodium, which was higher in the 24 m. eq./L. NO_3 (N_2) series.

* Present address : Department of Botany, The University of Lucknow, U.P., India.

The other nutrient constituents were as normally given in the Long Ashton complete nutrient solution (2) and the phosphate level was the same for all treatments.

The molybdenum levels were as follows :

Mo 1	2	3	4	5	6	7	8	
0·000005	0·00005	0·0005	0·005	0·05	0·48	4·8	19·2	p.p.m.

These levels represent mainly 10-fold increments from the " nil " level (Mo_1) which was estimated (2, 5) to provide approximately 0·000005 p.p.m. Mo.

All treatments were commenced at sowing on 6th June, 1951. Fresh solution was given weekly or daily, according to growth, for the duration of the work. About 30 seeds were sown in each pot and seedlings were thinned at frequent intervals until four plants remained in Mo_1 treatments and two in the other treatments. There were two pots per treatment in each of two blocks.

A small subsidiary experiment was begun shortly after the main one to examine further the effects of high molybdenum supplies. Nitrogen was given at 9·5 or 29·5 m. eq. NO_3, and molybdenum at 9·6, 19·2, 38·4 and 76·8 p.p.m. ; these plants were harvested after 10 weeks growth.

Pest control.

This became an important feature of the work. Mealy aphid was partially controlled by spraying with recrystallized D.D.T. suspension 0·1 per cent. in glass-distilled water or with a 0·1 per cent. solution of redistilled nicotine at weekly intervals using all-glass spraying apparatus. Cabbage-white butterfly caterpillars were removed by daily hand-picking and all plants were carefully examined individually. This was regarded as most important, to avoid possible confusion with the appearance of whiptail symptoms in some circumstances.

Growth response.

Yields of samples drawn at intervals and at the end of the experiment were determined as fresh material and after oven drying at 90° C. Areas of cotyledons at 2 weeks and of the largest expanded leaves at 52 days growth, in each treatment, were measured on leaf tracings.

Molybdenum content.

Molybdenum was determined in dried material after thorough grinding in a Pyrex mortar and wet digestion with nitric and perchloric acids. The dithiol method of Piper and Beckwith (13) was used for most samples, but small samples from severe deficiency treatments were assayed by the *Aspergillus niger* method (5). In several instances both methods were used on the same material with reasonable agreement.

RESULTS.

Visual symptoms.

Typical symptoms of molybdenum deficiency, namely mottling and cupping, observed in previous work with brassica crops (4, 7), appeared 3 weeks after sowing at both Mo_1 and Mo_2 levels. These symptoms progressed as expected from previous observations (7) and were followed by pronounced chlorosis, leaf marginal wilting and scorching, and withering of older leaves in plants at the Mo_1 level. This cycle of symptoms persisted in successive leaves in most plants grown at the Mo_1 level for

the duration of the experiments. These symptoms are termed *primary* symptoms to distinguish them from others which are termed *secondary* symptoms. These comprise the whiptail syndrome, and their origin and development are considered in more detail below. At the Mo_2 level the primary symptoms, which also appeared, mainly disappeared again after 2–3 weeks. Increase in the nitrate level from N_1 to N_2 accentuated the primary symptoms at the Mo_1 and Mo_2 levels. Primary symptoms did not occur at Mo_3 or higher levels.

Secondary symptoms of leaf malformation (7), leading to whiptail, appeared first 52 days from sowing in the Mo_2/high nitrate plants and 4 days later in the low nitrate plants after an interim period during which these plants appeared mainly normal and symptomless. After 69 days the Mo_2/high nitrate plants were relatively large but showed typical whiptail symptoms characteristic of field specimens found on acid soils (11, 14, 15, 18) where molybdenum deficiency prevails. Representative examples are shown in Plate II a, c. Leaf malformation and growth were much reduced in the low nitrate plants and the forms in this group were not so closely similar to field specimens.

In the Mo_1 series some plants made temporary recovery later in the experiment. This recovery was followed by the appearance of severe whiptail symptoms as shown in Plate II b, and resembled the most acute conditions found in the field. Primary symptoms did not usually re-appear after such temporary recovery, and plants became uniformly green. Plants grown with high nitrate at the Mo_3 level showed mild leaf malformation later in the experiment, and had relatively wide leaf angles (Plate II d). No other treatments produced leaf abnormalities. Curd formation was suppressed at the Mo_1 level and at the Mo_2 level with low nitrate. Curds were absent or small and brown at the Mo_2 level with high nitrate, and were subdivided by numerous bracts at the Mo_3 level. Typical plants grown at the Mo_1 and Mo_2 levels with low or high nitrate are shown in Plate I, f, g.

Development of whiptail symptoms. The symptoms of whiptail in cauliflower or broccoli plants growing in molybdenum deficient acid soils in the field have been adequately described (14, 15, 18), and similar symptoms have been recorded for molybdenum deficient cauliflowers grown in sand culture (3, 4). A few points merit further attention at this stage. First, the appearance of the true whiptail habit was always preceded by an initial white chlorosis followed by localized necrosis in from one to several small interveinal areas of a young rapidly expanding leaf, often in a relatively vigorous plant. This stage is shown in Plate I a, c. It was sometimes confined to a single leaf and seldom affected more than three leaves in succession. When the leaves expanded, the necrotic spaces perforated and also expanded with the leaf, producing irregular angular holes in the lamina as in Plate I b. Second, as the condition became more advanced the interveinal breakdown was succeeded by marginal necrosis, beginning in a narrow zone and then involving varying amounts, from a small part, up to the whole of the very young leaf in a membranous, brown and sometimes deliquescent tissue which rapidly disintegrated (Plate I b, e). Elongation of the midrib at the various stages described produced malformed leaves ranging from those with a marginal tear to bare midribs entirely devoid of lamina. Death of leaf tip growing points, breakdown of rudimentary leaves and death of the terminal growing point occurred in severe stages. The extent and times of occurrence of this sequence of effects interacted to vary the general form of the plants, producing the different examples shown in Plates I d, e ; II a, b, c.

The initial perforation symptoms, followed usually by the others, and culminating in whiptail, are termed secondary symptoms. They are referred to thus and are used as criteria of molybdenum deficiency in the later work to be described separately in which they were consistent in all respects with the observations reported here and previously (4, 6, 7). The sequence of symptoms and their ultimate effects were characteristic and could be distinguished from any effects due to occasional injury by undetected caterpillars.

Anatomical effects.

Leaves showing the initial interveinal chlorosis were embedded, sectioned and stained by haematoxylin or safranin and light green. Examination showed that cells in the abnormal areas were less firmly held together than usual and often tended to separate on sectioning. In some instances the epidermis parted easily from the underlying palisade tissues. It appeared that the middle lamella was either abnormal or defective, because staining of this region by either method became progressively weaker and narrower in section toward the centre of abnormal areas and, in advanced stages, the middle lamella was either invisible or non-existent in areas where the parenchyma cells were easily parted.

It is noteworthy that in *ll* instances, leaf malformation in whiptail was preceded by, and probably resulted directly from, previous tissue breakdown of the type described above.

Leaf area.

Earlier work (6) suggested that plants affected by sub-acute molybdenum deficiency may have larger leaves than normal during early growth. This suggestion was tested here by measuring areas of fully expanded cotyledons and later of the largest expanded leaf at a stage when whiptail symptoms were clearly evident but before they became severe. There were no significant effects of molybdenum supply on cotyledon area, but nitrate level affected their mean area as follows :

High nitrate : 2·685 sq. in. ; low nitrate : 1·759 sq. in. ; ($P<0·01$).

Maximum leaf areas, on the other hand, appeared to be related to molybdenum supply in the manner previously suggested as well as by nitrate level, as shown by Table I.

Table I.

Mean areas in sq. in. of largest leaf in relation to Mo and NO_3 levels (4–8 replicates).

Mo level	1	2	3	4	5	6	7	8
Low NO_3	15·7	24·3	**51·8**	35·3	33·4	39·7	35·9	32·7
High NO_3	34·8	**199·4**	83·7	85·2	78·5	93·9	132·2	117·0

The effect was outstanding with high nitrate at the Mo_2 level and was evident also in the low nitrate series at the Mo_3 level.

Molybdenum excess.

Symptoms of molybdenum excess appeared for a short period in a few plants at the Mo_7 (4·8 p.p.m.) level and generally at the Mo_8 (19·2 p.p.m.) level. The main

effect was the development of a blue pigment (19) in cotyledons and foliage or in the stems. In leaves the pigment was often present in localized areas (Plate I h), and appeared as blue granular inclusions mainly in the epidermal cells of the lower surface. In stems the blue granules were concentrated in the outer layers of the cortex and were practically absent from other tissues.

YIELDS.

The effects of molybdenum and nitrate levels on yields are shown in Table II for 65 days growth and in Fig. 1 for 90 and 180 days growth respectively. The values for significance at the 5 per cent. level for differences between any two points in the growth curves in Fig. 1 are 13·9 and 73·7 g. for 90 and 180 days respectively.

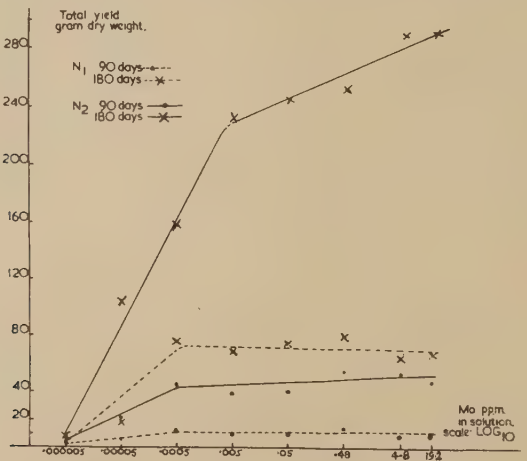

FIG. 1.

Effects of increasing concentration of molybdenum on yields of cauliflower plants grown in sand culture with low and high nitrate levels; N_1 6 m. eq./L., N_2 24 m. eq./L. at two stages of growth; 90 and 180 days from sowing.

The following conclusions are drawn from the results. The molybdenum level beyond which yields did not increase or increased only slightly, was higher with high nitrate than with low nitrate supply for fully grown plants (Fig. 1).

Growth was related almost linearly to the logarithm of the molybdenum concentration in the nutrient solution up to the Mo_3 or Mo_4 level, beyond which progressive increase in growth was less or nil, according to nitrate level. The progressive increases in total yield and in yield of curd *beyond* the Mo_4 level in the high nitrate series at both 90 and 180 days are interpreted as indicating a positive effect although the increase was less than that required for significance by a narrow margin. This conclusion is supported by a similar increase in yield between 9·6 and 19·2 p.p.m. Mo recorded for the high nitrate series in the subsidiary experiment before marked toxicity effects supervened at 38·4–76·8 p.p.m., as shown in Table III. Yields of fresh material, not shown here, were significantly greater at the Mo_6 level than at the Mo_4 level.

TABLE II.

Yield (g. dry weight) and molybdenum content of expanded leaves (p.p.m. in dry matter) of cauliflower plants at 65 days growth.

Mo level p.p.m.		Yield		Mo content p.p.m.	
		6 m. eq. NO_3	24 m. eq. NO_3	6 m. eq. NO_3	24 m. eq. NO_3
1	0·000005	1·5	2·3	0·09	0·10
2	0·00005	1·5	6·5	0·10	0·10
3	0·0005	2·8	6·2	0·27	0·32
4	0·005	2·7	7·8	1·02	0·93
5	0·05	2·2	9·1	6·46	6·93
6	0·48	3·6	12·9	36·4	74·2
7	4·8	2·8	10·3	655	1,206
8	19·2	2·6	9·4	1,829	3,816

Molybdenum levels of 100 to 1,000 times those permitting vigorous growth were not appreciably toxic as judged by yields and the ratio of molybdenum levels producing acute deficiency to those causing marked toxicity symptoms was of the order of 10^6.

MOLYBDENUM STATUS.

Molybdenum in dry material.

The results, shown in Table II for 65 days and in Figs. 2–5 for 90 and 180 days growth, suggest the following conclusions regarding the effects of molybdenum and nitrate supply on molybdenum uptake and distribution in the plants during growth.

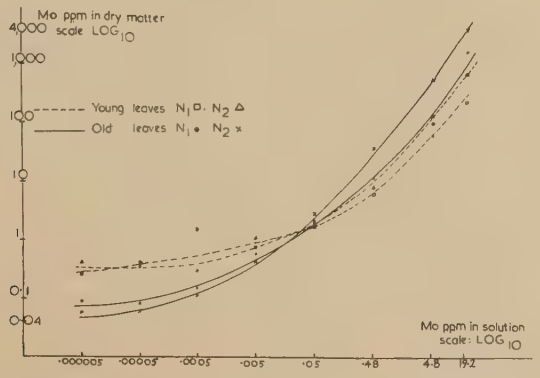

FIG. 2.

Molybdenum content in dry matter of young and old leaves of cauliflower plants grown for 90 days at two levels of nitrate: N_1 6 m. eq./L., N_2 24 m. eq./L. with increasing concentrations of molybdenum. Data represented on logarithmic scales.

Molybdenum concentration in dry matter remained relatively low from 0·000005 up to 0·05 p.p.m. (Mo_5) at 65–90 days growth and was correspondingly low from 0·000005 up to 0·005 p.p.m. (Mo_4) at 180 days growth. Above these levels of supply the molybdenum concentration rose rapidly (Table III, Figs. 2, 3). Over the same

ranges of molybdenum supply, the ratio of the concentration in the nutrient solution to that in leaf dry matter fell sharply from about 10,000–20,000 to 100–250 and then became nearly steady. The molybdenum levels at which accumulation in the foliage increased rapidly corresponded approximately with those levels beyond which the linear relationship between growth and the logarithm of the molybdenum supply no longer applied (Fig. 1).

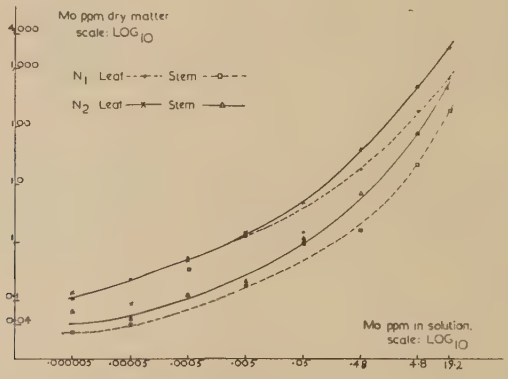

FIG. 3.

Molybdenum content in dry matter of mid-stem leaves and stems of cauliflower plants grown for 180 days at two levels of nitrate : N_1 6 m. eq./L., N_2 24 m. eq./L. with increasing concentrations of molybdenum. Data represented on logarithmic scales.

Transformation of the molybdenum concentrations in dry matter to a logarithmic form produced uniformly concave curves (Figs. 2–4). When the *total* molybdenum uptake at 180 days was plotted against molybdenum level using logarithmically transformed data the curve appeared to approximate to a straight line (Fig. 5), in the high nitrate series, and possibly also in the low nitrate series but with some discontinuity between 0·0005 and 0·05 p.p.m. Mo. The total molybdenum content of leaves only was closely correlated with that in whole plants.

The effect of nitrate supply on molybdenum status varied with the molybdenum level. It was negligible up to the Mo_4 or Mo_5 values but, above these, high nitrate resulted in an increased concentration of molybdenum in dry matter. This effect was also found in the subsidiary experiment (Table III), but the relative accumulations were lower.

Molybdenum distribution.

The concentrations of molybdenum in leaves, stems, roots and curds at 180 days growth were similar at molybdenum levels up to Mo_4 or Mo_5 (Figs. 3, 4). Above these levels, leaves had the highest concentrations, followed closely by roots and then by stems and curds at substantially lower values. Young and old leaves were compared at 90 days growth (Fig. 2). Young leaves contained notably higher concentrations of molybdenum than the old ones at deficiency and threshold levels up to Mo_4 but contained substantially less (with one exception) at the higher, luxury consumption, levels of molybdenum.

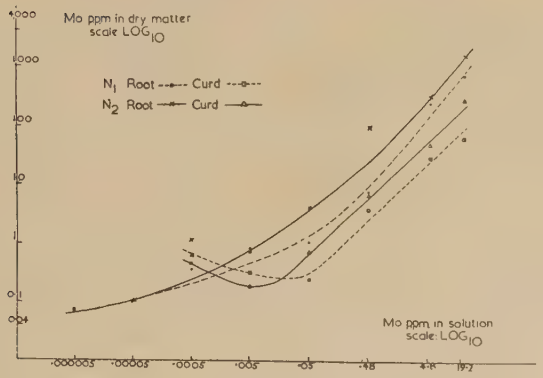

Fig. 4.

Molybdenum content in dry matter of roots and curds of cauliflower plants grown for 180 days at two levels of nitrate: N_1 6 m. eq./L., N_2 24 m. eq./L. with increasing concentrations of molybdenum. Data represented on logarithmic scales.

The distribution within the leaf was also examined. At 0·00005 p.p.m. Mo the concentrations in leaf margins (5 mm. wide), central interveinal areas and midrib were respectively 0·15, 0·08 and 0·14 p.p.m. At 0·05 p.p.m. Mo the values were respectively 3·3, 5·8 and 1·2 p.p.m.; at 19·2 p.p.m. Mo they were 3,215, 1,745 and 630 p.p.m. respectively for the three regions. It will be noted that under deficiency conditions the minimum concentration was in the region where the first signs of the whiptail syndrome developed.

In order to learn if the blue parts of leaves of high molybdenum plants contained locally excessive concentrations, a number of such parts were cut out from leaves of

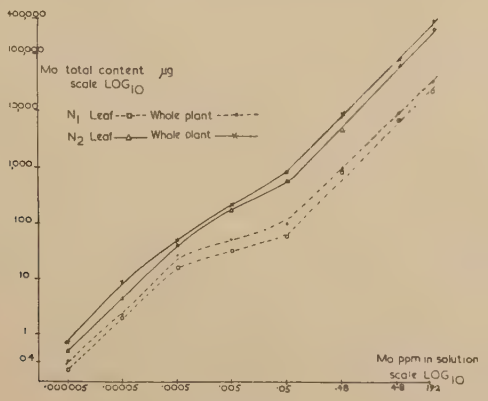

Fig. 5.

Relation between logarithm of molybdenum concentration in nutrient solution (p.p.m.) and logarithm of total molybdenum content (µg) of whole cauliflower plants and of their leaves with low (N_1) or high (N_2) nitrate supply.

plants given 6, 9·5, 24 and 29·5 m. eq./L. NO_3 and 19·2 to 76·8 p.p.m. Mo. Similar portions of green tissue were taken from the *same* leaves for comparison. Values found from 5 treatments ranged as follows :

" Blue " parts 1,518 to 8,085 p.p.m., mean 4,146 p.p.m.
Green parts 2,852 to 7,455 p.p.m., mean 4,846 p.p.m.

There was, therefore, no significant difference between the two sets.

TABLE III.

Yields (g. dry weight) and molybdenum concentration in foliage (p.p.m. in dry matter) of cauliflower plants grown at high Mo levels in subsidiary experiment.

Mo p.p.m. in solution	9·5 m. eq./L. NO_3		29·5 m. eq./L. NO_3	
	Yield	p.p.m. Mo	Yield	p.p.m. Mo
9·6	9·8	63·4	21·2	213·6
19·2	8·9	76·4	26·2	566·8
38·4	6·1	207·7	15·5	1239·0
76·8	6·7	500·0	13·2	2294·4

DISCUSSION.

The production of whiptail or secondary symptoms in plants given 0·00005 p.p.m. Mo as compared with the persistence of mainly primary molybdenum deficiency symptoms of mottling, cupping and scorching in old leaves of plants given 0·000005 p.p.m. Mo, confirms the previous suggestion (4, 7) that whiptail symptoms represent an intermediate effect between severe deficiency and normal growth in plants given nitrate nitrogen. At such intermediate levels of molybdenum an abundant nitrogen supply is conducive to the production of these symptoms. The initially vigorous growth and mainly uniformly green appearance of these plants suggest that considerable nitrate assimilation occurred in the early stages of growth. Some other factor of metabolism may then have become the one limiting growth with the consequent tissue breakdown, leading to whiptail symptoms. Further discussion of this point is deferred to the later papers.

It is evident that manganese toxicity is not a necessary co-factor in the production of whiptail, although there is little doubt that under field conditions manganese may accentuate or even induce molybdenum deficiency or depress molybdenum uptake by plants (1, 9, 10).

Yield data suggested that the nitrate supply is an important factor affecting the level of the molybdenum supply beyond which growth shows no further increase. Extra nitrate supply resulted not only in extra growth but also in a higher molybdenum requirement. Higher nitrate supply, however, significantly increased yields even at the most severely limiting molybdenum level.

The remarkable range of about 10^5 to 10^6-fold between acute deficiency and toxicity levels of molybdenum in the nutrient solution for cauliflower merits comment. It exceeds by a wide margin that known at present for any other micro-nutrient element, although normal requirements are apparently minute by comparison with other known essential elements. The corresponding range of molybdenum concen-

tration in the plants also exceeds by about 1,000-fold that known for other elements, e.g. manganese, when producing comparable effects of deficiency and toxicity. Under certain circumstances, however, not yet elucidated, high molybdenum supplies produced toxic effects on the plants without the expected correspondingly great increase in the internal concentration.

The results obtained here have provided the first quantitative estimates of the molybdenum supply levels associated with marked deficiency and with threshold toxicity effects respectively. These may be stated as approximately between 0·000005 and 0·00005 p.p.m. for deficiency effects and 20 p.p.m. Mo for toxicity.

The initially great responses in yields produced by the lower molybdenum increments contrasted sharply with the very limited changes in concentration in the dry matter of these plants over the same molybdenum range. Rapid increases in concentration occurred when growth increments became small (Table III and Figs. 1–4). These relationships account for many observations made under field conditions where normal and deficient plants have shown only small differences in molybdenum content. Examination of the total molybdenum uptake, however, indicated a more rational relationship as shown in Fig. 5, in which the logarithmically transformed total values show a probable linear relationship. The range of molybdenum levels over which there was possibly some discontinuity, more particularly in the N_1 set, coincides approximately with those over which there were sharp changes in gradients of the growth curves, shown in Fig. 1.

Analytical studies provided two other interesting results. First it would appear that the relative differences in molybdenum status of young and old leaves did not coincide with those which would be expected if the observed distribution of whiptail and secondary symptoms resulted merely from a difference in total molybdenum status of old and young leaves of deficient plants. Second, the localized blue areas in leaves were not associated with localized accumulation of molybdenum as far as macroscopic tests could determine in spite of their being attributed to specific molybdenum compounds (19).

One point regarding the interpretation of some of our results in relation to the design of the experiment requires comment in the light of the results of Stout *et al.* (17) not available to us at the time the experiment was planned. These workers showed beyond doubt that sulphate depresses molybdenum uptake by some crops without necessarily decreasing yields. It is, unfortunately, not possible at present to distinguish in our experiments between the possible effects of sulphate and nitrate level, and certain conclusions drawn from effects of different nitrate supply regarding *molybdenum concentration in plants* might be due in greater or lesser part to effects of sulphate. With regard to effects of nitrate level on growth in relation to optimum molybdenum supply, our conclusions are not affected by the possible interference of sulphate as a factor, since the points at which the growth response is diminished sharply correspond to a *higher* molybdenum level with the high nitrate than with low nitrate, whereas the sulphate effect would exert an opposite influence by checking the capacity for molybdenum uptake at any given level. Evidence that the different effects of solutions providing the different nitrate supplies on molybdenum concentrations within the plants were due, at least in part, to differences in nitrate supply, is provided by the fact that the nitrate effect was negligible or even reversed at certain stages in plants grown with low or normal levels of molybdenum and only became marked at luxury consumption levels.

Stout *et al.* (17) noted (p. 78, in footnote to Table VIII, *loc. cit.*) that the amount of molybdenum accumulated by a plant is probably nearly a direct function of its size. Our experiments have confirmed that molybdenum accumulation is a function of size, and indicate that the relationship is probably a log. linear function for cauliflower.

SUMMARY.

1. Cauliflower plants, variety Majestic, were grown in sand cultures at low and high nitrate levels of 6 and 24 m. eq./L. with 8 levels of molybdenum ranging from 0·000005 p.p.m. to 19·2 p.p.m.

2. At 0·000005 p.p.m. molybdenum deficiency symptoms were mainly mottling, cupping and scorching of older leaves, with instances of whiptail after partial recovery. Whiptail symptoms, typical of those seen under field conditions, developed with high nitrate supply and 0·00005 p.p.m. Mo.

3. The production of whiptail symptoms was preceded by a characteristic series of events beginning with localized interveinal tissue breakdown in young leaves. This breakdown was associated initially with an apparent loss of the middle lamella in groups of cells in affected areas. The final leaf form produced depended on the location and extent of the tissue breakdown that had occurred during the continued leaf expansion.

4. The area of the largest expanded leaf was a maximum at molybdenum levels intermediate between those producing severe deficiency and the normal levels producing maximum growth.

5. Blue granules developed in leaves of plants given excess of molybdenum (19·2 p.p.m. or more). They were located mainly in leaf lower epidermis and stem outer cortical regions.

6. The high nitrate supply increased the molybdenum requirement and the molybdenum level up to which the growth response was linearly related to the logarithm of the molybdenum level. High nitrate also increased growth at the most acute molybdenum deficiency level. The growth response diminished sharply beyond 0·005 p.p.m. Mo.

7. Molybdenum content of leaves and other parts increased from less than 0·1 to 4,000 p.p.m. approximately, with increasing molybdenum supply, but the changes were small over the region of the linear growth response. Above this the molybdenum concentration in dry matter increased rapidly.

8. Nitrate supply did not affect molybdenum content at the lower levels, but high nitrate increased molybdenum content at the high molybdenum levels.

9. Young leaves contained more molybdenum at deficiency levels and less at normal to excess levels than old leaves. The development of whiptail in young leaves could not be explained, therefore, in terms of distribution of total molybdenum. Parts of leaves with blue colour caused by excess molybdenum did not contain more molybdenum than similar green portions of the same leaves.

10. The logarithm of total molybdenum uptake by mature plants was related by a probably linear function to the logarithm of the molybdenum supply.

PLATE I

a, b, c Initial stages in the development of whiptail symptoms. Chlorotic areas ; a and c (right) leading to irregular interveinal perforations during expansion and to necrosis in marginal areas ; b and c (left).

d, e Irregular marginal necrosis with continued elongation of midrib ; death of leaf tip of rear leaf in d. Later stages than a—c.

f, g Relative effects of 0·000005 (left) and 0·00005 p.p.m. Mo (right) on growth with low nitrate (f) and high nitrate supply (g). Leaf malformation most evident with 0·00005 p.p.m. Mo.

h Areas of blue pigment in leaf of plant grown with 19·2 p.p.m. Mo.

[face page 288

PLATE II

a Typical whiptail condition produced at 0·00005 p.p.m. Mo and high nitrate supply; note well expanded older leaves and absence of mottling.

b Severe whiptail occurring after partial recovery from primary symptoms produced with 0·000005 p.p.m. Mo.

a and b correspond closely to field specimens.

c Severe whiptail and death of the growing point in plant grown with 0·00005 p.p.m. Mo and high nitrate.

d Slight leaf malformation and "wide" leaf-stem angles in plant grown with 0·0005 p.p.m. Mo and high nitrate.

ACKNOWLEDGMENTS.

The provision of an Overseas Research Fellowship by the U.P. Government, India, to S. C. Agarwala from 1950 to 1952 is most gratefully acknowledged.

The writers wish to thank Mr. G. H. Jones, A.R.P.S., for the photographic work, and Miss J. E. Mores for analytical assistance.

REFERENCES.

(1) *Anderson, A. J.*, and *Spencer, D.* (1950). Molybdenum in nitrogen metabolism of legumes and non-legumes. Aust. J. sci. Res., **13,** 3, 414.

(2) *Hewitt, E. J.* (1952). The use of sand and water culture methods in the study of plant nutrition. Tech. Commun. Bur. Hort. E. Malling. **22.**

(3) ——— and *Agarwala, S. C.* (1951). Production of whiptail in cauliflower grown in sand cultures. Nature, **167,** 733.

(4) ——— (1953). The importance of molybdenum in the nutrition of horticultural plants. 13th Internat. hort. Congress, London, 1952. *Proc.* **1**, 375.

(5) ——— and *Hallas, D. G.* (1951). The use of *Aspergillus niger* (Van Teigh.) M. strain as a test organism in the study of molybdenum as a plant nutrient. Plant & Soil, **3,** 366.

(6) ——— and *Jones, E. W.* (1947). The production of molybdenum deficiency in plants in sand culture with special reference to tomato and brassica crops. J. Pomol., **23,** 254.

(7) ——— and *Bolle-Jones, E. W.* (1952). Molybdenum as a plant nutrient. I. The influence of molybdenum on the growth of some brassica crops in sand culture. J. hort. Sci., **27,** 245.

(8) ——— ——— (1952). Molybdenum as a plant nutrient. II. The effect of molybdenum deficiency on some horticultural and agricultural crop plants in sand culture. J. hort. Sci., **27,** 257.

(9) ———, *Jones, E. W.*, and *Nicholas, D. J. D.* (1948). The production of molybdenum deficiency in plants in sand culture, with special reference to tomato and Brassica crops. Ann. Rep. Long Ashton Res. Sta., 1947, 70.

(10) *Millikan, C. R.* (1948, 1949). Lower leaf scorch of flax. J. Dep. Agric. Victoria (Australia), **46,** 511, 566 ; Ibid., **47,** 37.

(11) *Mitchel, K. J.* (1945). Preliminary note on the use of ammonium molybdate to control whiptail in cauliflower and broccoli crops. New Zealand J. Sci. and Tech., **27A,** 287.

(12) *Mulder, E. G.* (1948). Importance of molybdenum in the nitrogen nutrition of micro organisms and higher plants. Plant & Soil, **1,** 94.

(13) *Piper, C. S.*, and *Beckwith, R. S.* (1948). A new method for the determination of small amounts of molybdenum in plants. J. Soc. chem. Ind., **67,** 374.

(14) *Plant, W.* (1950). The control of whiptail in broccoli and cauliflower. J. hort. Sci., **26,** 109.

(15) ——— (1950). The control of "Whiptail" in broccoli and cauliflower. Agriculture (J. Min. Agric. U.K.), **57,** 130.

(16) *Stout, P. R.*, and *Meagher, W. R.* (1948). Studies of the molybdenum nutrition of plants with radioactive molybdenum. Science, **108**, 471.

(17) ———, ———, *Pearson, G. A.*, and *Johnson, C. M.* (1951). Molybdenum nutrition of crop plants. I. The influence of phosphate and sulphate on the absorption of molybdenum from soils and solution cultures. Plant & Soil, **3**, 51.

(18) *Waring, E. J.*, *Wilson, R. D.*, and *Shirlow, N. S.* Whiptail of cauliflower ; control by the use of ammonium molybdate and sodium molybdate. Agric. Gaz. New South Wales, Dec. 1948–Jan. 1949. New South Wales Dept. Agric. misc. Pubn. no. 3, 354.

(19) *Warington, K.* (1937). Observations on the effect of molybdenum on plants with special reference to the Solanaceae. Ann. appl. Biol., **24**, 475.

(20) *Wilson, R. D.*, and *Waring, E. J.* (1948). Some observations and experiments concerning the role of molybdenum in the nutrition of the cauliflower plant. J. Australian Inst. agric. Sci., **14**, 141.

(*Received* 23/1/54.)

MOLYBDENUM AS A PLANT NUTRIENT

IV. THE INTERRELATIONSHIPS OF MOLYBDENUM AND NITRATE SUPPLY IN CHLOROPHYLL AND ASCORBIC ACID FRACTIONS IN CAULIFLOWER PLANTS GROWN IN SAND CULTURE

By S. C. AGARWALA* and E. J. HEWITT
A.R.C. Unit of Plant Nutrition (Micronutrients), Long Ashton Research Station, University of Bristol

The previous paper in this series (1) reported effects of molybdenum and nitrogen supply on the growth, whiptail development and molybdenum status of cauliflower plants grown in sand culture with 8 levels of molybdenum ranging from 0·000005 to 19·2 p.p.m. and with 6 or 24 m. eq./L. nitrate nitrogen. It was shown that molybdenum supply had large effects on growth from 0·000005 to 0·0005 p.p.m. Mo when 6 m. eq./L. NO_3^+ was given in the nutrient solution. With 24 m. eq./L. NO_3^+ additional molybdenum increased growth markedly up to 0·005 p.p.m. Mo and then less effectively up to 4·8 or 19·2 p.p.m. Growth was always greater with the higher nitrogen supply. The symptoms of molybdenum deficiency varied in nature, as well as in severity, with molybdenum level, and whiptail was associated mainly with a molybdenum supply of 0·00005 p.p.m. There were regular curvilinear relationships between the logarithms of molybdenum supply in solution and contents in dry matter, and nearly linear relationships between logarithms of molybdenum supply and total content per plant.

The present paper describes changes produced in the content of chlorophyll, ascorbic and dehydroascorbic acids in plants grown in this experiment. Effects of nitrate and molybdenum status on ascorbic acid content had been reported earlier (6) and detailed confirmation was desired. The possible interrelationships with carbohydrate fractions and nitrate assimilation will be considered in the next paper.

EXPERIMENTAL.

Methods.

Culture methods.

Details of methods used to grow the plants have been described in previous papers (1, 5). The lower nitrate supply (N_1) provided 6 m. eq./L. nitrate nitrogen, and the higher (N_2) provided 24 m. eq./L.

Chlorophyll.

Leaf laminae were separated from the midribs, cut into small pieces and a weighed sub-sample, 0·5–1 g., was frozen in solid carbon dioxide. The sample was macerated in 85 per cent. acetone with carborundum powder and 100 mg. calcium carbonate in a small motor-driven Pyrex glass macerator. Chlorophyll was then estimated by the method used by Bolle-Jones and Notton (2).

* Present address: Department of Botany, The University of Lucknow, U.P., India.

Ascorbic acid and associated fractions.

Ascorbic acid was estimated by rapid titration of 5 per cent. metaphosphoric acid extracts of fresh tissues with 2,6-dichlorophenol-indophenol dye, standardized each time with pure ascorbic acid as described by Harris and Ray (1953) (3). Copper-free water was used throughout and extracts awaiting analysis were stored in darkness at 0°–4° C. No changes in ascorbic acid content occurred during the few hours for which storage was necessary. Possible interference by nitrite was avoided by the inclusion of amido-sulphonic acid during extraction, as suggested by Mapson (9).

Dehydroascorbic acid was determined by difference from total ascorbic acid found after reduction of dehydroascorbic acid by hydrogen sulphide at pH 3 in the presence of added sodium citrate, removing hydrogen sulphide by gassing with nitrogen and stabilizing by the addition of sulphuric acid to pH 1–2.

Cysteine and sulphite interference were estimated in aliquots by loss of reducing value after treatment with formaldehyde as described by Mapson (1943) (10). Other reductones were assumed to be absent from fresh tissues (10) and dihydroxymaleic acid content was negligible, as shown by stability in storage.

In later work, ascorbic acid values were estimated without reference to the low content of cysteine or sulphite, since the latter amounted to only 5–10 per cent. of the total reducing value.

RESULTS.

Chlorophyll.

Results of chlorophyll estimations made at 30 and 55 days growth and at 86 and 172 days growth are shown in Figs. 1 and 2 respectively. Four conclusions are drawn from the data in Fig. 1 :

(*a*) Chlorophyll content increased markedly (P=0·01) between 0·000005 and 0·0005 p.p.m. Mo.

(*b*) There were no appreciable changes over the range 0·005 to 0·48 p.p.m. Mo.

(*c*) There was a tendency for chlorophyll content to decrease at 4·8 or 19·2 p.p.m. Mo.

(*d*) Chlorophyll content was slightly greater with the higher nitrate supply (N_2) at the optimum molybdenum levels but was markedly less with the higher than with the lower nitrate supply at molybdenum deficiency levels. There was possibly a depressive effect due to nitrate at the highest molybdenum levels.

Data in Fig. 2 show that young leaves contained much more chlorophyll than did mature ones at molybdenum deficiency levels but less at higher levels (0·48 p.p.m. Mo). Chlorophyll content of young leaves did not in fact show any response to molybdenum at the low nitrate level. At the higher nitrate level there was a response to molybdenum, but it occurred over an incremental range only one-tenth of that which was effective for mature leaves. At the more advanced stages of growth represented in Fig. 2, high nitrate consistently produced a higher chlorophyll content than low nitrate. In other respects the curves were similar in character to the earlier ones, except that there was at 172 days no marked decrease at the 19·2 p.p.m. Mo level and also that the general chlorophyll content had decreased with age over the optimal molybdenum range.

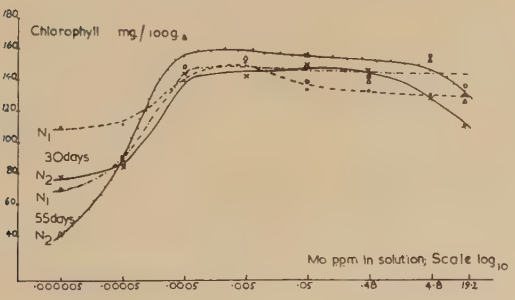

FIG. 1.

Effects of molybdenum and nitrate supplies on chlorophyll content (mg./100 g. fresh weight) in midstem leaves of cauliflower at 30 and 55 days growth. N_1 : low nitrate. N_2 : high nitrate. Mo supply represented on a logarithmic scale.

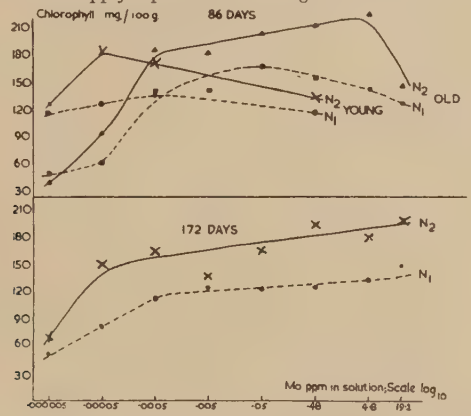

FIG. 2.

Effects of molybdenum and nitrate supplies on chlorophyll content (mg./100 g. fresh weight) in young and mature leaves of cauliflower at 86 days and in mature leaves at 172 days growth. N_1 : low nitrate. N_2 : high nitrate. Mo supply represented on a logarithmic scale.

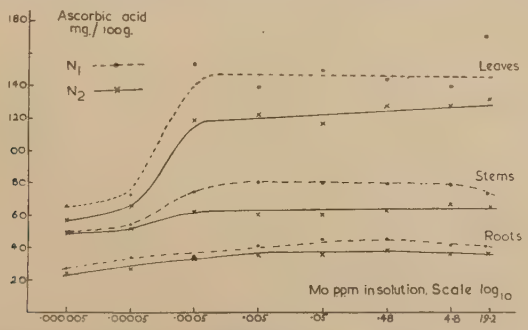

FIG. 3.

Effects of molybdenum and nitrate supplies on ascorbic acid content (mg./100 g. fresh weight) in leaves, stems and roots of cauliflowers at 53 days growth. N_1 : low nitrate. N_2 : high nitrate. Mo supply represented on a logarithmic scale.

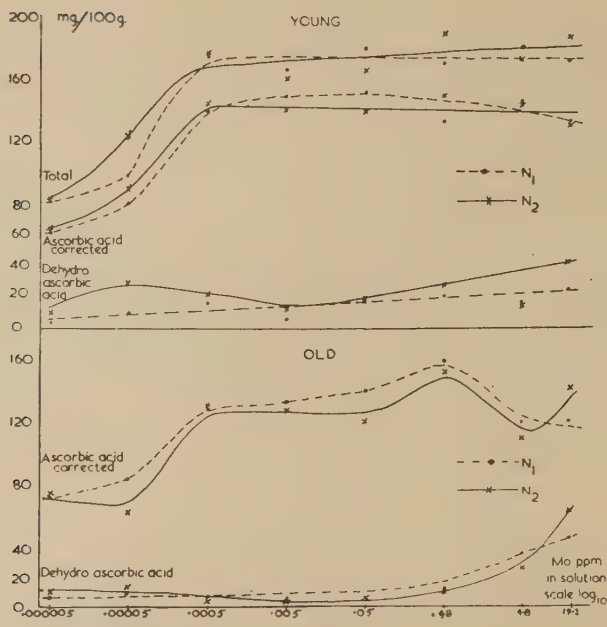

FIG. 4.

Effects of molybdenum and nitrate supplies on ascorbic acid content corrected for reductones and dehydroascorbic acid content (mg./100 g. fresh weight) in young and mature leaves of cauliflowers at 77 days growth. N_1 : low nitrate. N_2 : high nitrate. Mo supply represented on a logarithmic scale.

Ascorbic acid and associated fractions.

Samples were taken at 17, 29, 53, 77, 92 and 172 days growth for estimation of these fractions. Data obtained at 17 and 29 days growth are shown in Table I, while data for the other times are shown graphically in Figs. 3–7. The following conclusions are drawn :

Ascorbic acid. (*a*) Molybdenum deficiency consistently resulted in a marked and usually highly significant decrease ($P=0{\cdot}05$–$0{\cdot}001$) in ascorbic acid in leaves at all stages of growth, and at both nitrate levels.

(*b*) The effect was evident as early as 17 days after sowing (Table I), a few days before visual symptoms were discernible.

(*c*) Increased molybdenum supply from 0·000005 to 0·0005 p.p.m. resulted in appreciable increase in ascorbic acid. The amount of the increase became progressively larger in mature leaves with age, Figs. 3–6, so that the shape of the response curve changed.

(*d*) Concentrations of ascorbic acid were greatest in leaves, less in stems and least in roots, Fig. 3. Effects of molybdenum supply were greater in aerial parts than in roots (Table I and Fig. 3). Young leaves generally contained higher concentrations of ascorbic acid than mature leaves, but differences were not great and

there were exceptions (Fig. 4). Curds contained only low concentrations and showed scarcely any molybdenum effect (Fig. 6).

(*e*) Plants grown with the lower nitrate supply contained more ascorbic acid than those grown with the higher nitrate supply with few exceptions. These effects of nitrate supply were significant (P=0·05–0·001) at 53, 77, 92 and 172 days growth, except in young leaves.

There was no appreciable increase in ascorbic acid concentration with molybdenum supply above 0·0005 p.p.m., with possible exceptions at 77 days for old leaves, N_1 (Fig. 4), and 172 days growth (Fig. 6) (P=0·05).

There were occasionally slight decreases at the highest molybdenum levels, but these were seldom significant at the 5 per cent. level.

Table I.

Effect of molybdenum and nitrate supply on ascorbic acid content (mg. per 100 g. fresh weight) of shoots and roots of cauliflower seedlings.

Age	17 days				29 days			
Mo level p.p.m.	Shoot		Root		Shoot		Root	
	Nitrate level		Nitrate level		Nitrate level		Nitrate level	
	6	24	6	24	6	24	6	24
0·000005	83·8	70·6	31·9	33·5	68·4	30·9	15·6	23·4
0·00005	91·2	73·8	32·5	28·8	76·1	42·9	24·7	15·6
0·0005	97·5	73·9	41·3	28·4	81·0	69·2	40·3	31·2
0·005	100·0	88·8	35·0	32·5	85·2	67·0	46·8	31·2
0·05	120·0	92·5	37·5	38·1	—	68·9	—	31·2
0·48	108·8	86·2	36·3	27·5	93·9	68·9	—	33·8
4·8	103·8	88·1	35·0	25·0	87·8	80·3	59·8	35·1
19·2	110·6	93·8	32·5	25·0	84·7	69·9	65·0	33·8

Dehydroascorbic acid. Dehydroascorbic acid content ranged from 5 to 20 per cent. of the total expressed as ascorbic acid and was normally less than 10 per cent. Effects of changes in either molybdenum or nitrate supplies were mainly small. There was a tendency, however, for dehydroascorbic acid concentration to increase at high molybdenum levels, whilst at deficiency levels there was practically no response (Figs. 4, 5, 6).

Dehydroascorbic acid/ascorbic acid ratio. The effect of treatments on the relative proportions of the two compounds are shown in Fig. 7. Data relating specifically to 172 days growth are shown, with curves for the means of 8 sets of estimations for each nitrate supply at different ages or from young and mature leaves. It is concluded that the ratio DHA/AA is minimum for the intermediate molybdenum levels, especially those regarded as adequate for, but not in any way toxic to growth. The higher ratios at deficiency levels are due to greater decreases in ascorbic acid than in dehydroascorbic acid, whilst at high molybdenum levels similar high ratios are due mainly to increases in dehydroascorbic acid accompanied by slight decreases in ascorbic acid concentrations. Nitrate supply did not greatly affect this ratio, but there was possibly a general increase with extra nitrate supply. It is relevant to note that errors in estimation of dehydroascorbic acid were relatively magnified because values

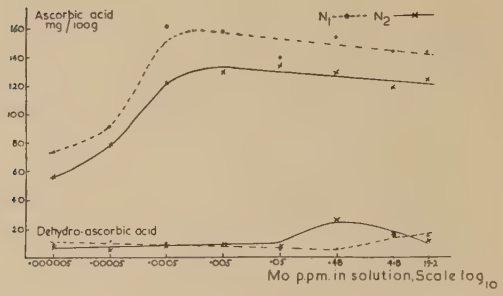

FIG. 5.

Effects of molybdenum and nitrate supplies on ascorbic and dehydroascorbic acid contents (mg./100 g. fresh weight) in leaves of cauliflower at 92 days growth. N_1 : low nitrate. N_2 : high nitrate. Mo supply represented on a logarithmic scale.

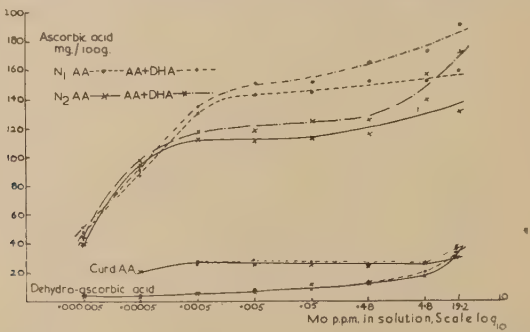

FIG. 6.

Effects of molybdenum and nitrate supplies on the ascorbic acid, dehydroascorbic acid and their total contents (mg./100 g. fresh weight) in leaves and on ascorbic acid in curds of cauliflower at 172 days growth. N_1 : low nitrate. N_2 : high nitrate. Mo supply represented on a logarithmic scale.

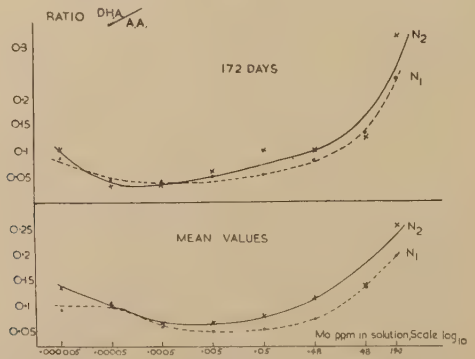

FIG. 7.

Effects of molybdenum and nitrate supplies on the ratio dehydroascorbic acid/ascorbic acid in leaves of cauliflower at 172 days and the mean values of the ratio for all estimations. N_1 : low nitrate. N_2 : high nitrate. Mo supply represented on a logarithmic scale.

for this were obtained by difference from two sets of estimations each susceptible to similar errors, and also because the values for dehydroascorbic acid were small compared with ascorbic acid.

Reductone fractions. The concentrations of such compounds as sulphite, cysteine, etc., estimated in the experiments reported in Table II, amounted only to about 3–8 per cent. of the total content calculated as ascorbic acid. Values as high as 10 per cent. of the total were rare.

There was no clear relationship between molybdenum or nitrate supplies and the reductone fraction. Sets of data for ascorbic acid obtained after correction for this possible interference, as shown in Fig. 4, were closely similar to the ascorbic acid results estimated without correction. Young leaves appeared to contain slightly more reductones than did mature leaves. It was concluded, using the rapid end-point procedure for ascorbic acid titrations, that the small amounts of these reductones present had no effect at all on the general trends described above.

Table II.

Concentration of cysteine and sulphite reductones (mg. per 100 g. fresh weight as ascorbic acid) at different stages of growth and their proportion as per cent. of ascorbic acid values at different molybdenum and nitrate levels.

Age	77 days				92 days	
Molybdenum level in solution, p.p.m.	Mature leaf		Young leaf		Mature leaf	
	Nitrate level		Nitrate level		Nitrate level	
	6 m. eq.	24 m. eq.	6 m. eq.	24 m. eq.	6 m. eq.	24 m. eq.
0·000005	4·3	7·8	6·2	7·9	2·5	3·8
% of AA	5·3	8·6	7·4	9·6	3·2	6·3
0·00005	3·3	5·5	5·3	4·5	1·5	3·3
% of AA	3·7	7·5	5·9	4·4	1·7	3·8
0·0005	6·3	13·8	17·4	11·0	14·4	9·9
% of AA	4·5	8·4	10·0	6·6	8·1	7·5
0·005	4·2	5·6	10·8	10·3	7·4	5·3
% of AA	3·0	5·0	6·4	6·2	4·5	4·0
0·05	5·3	6·4	12·2	9·5	7·4	8·0
% of AA	3·5	5·6	7·0	5·3	5·1	5·7
0·48	7·1	8·3	15·5	14·2	9·0	3·3
% of AA	4·1	4·8	8·5	8·2	5·5	2·5
4·8	12·5	11·5	18·0	17·4	8·0	2·5
% of AA	8·6	8·9	10·0	9·7	5·3	2·1
19·2	11·2	9·8	12·9	13·5	6·3	10·0
% of AA	7·8	5·9	8·1	8·6	4·3	7·6
Means	6·8	8·5	12·3	10·7	7·1	5·8
% of AA	5·1	6·8	7·9	7·3	4·7	4·8

DISCUSSION.

The results presented here fully confirm the earlier finding (6) that molybdenum supply has a pronounced effect on apparent ascorbic acid content. Evidence that the indophenol method used in this work does in fact indicate true ascorbic acid is not yet complete. However, it is generally considered (Mapson, 1943) (10) that the rapid indophenol titration method is reasonably specific for ascorbic acid if allowance is made for effects of cysteine reductones, reductic acids, dehydroxymaleic acid and hydroxytetronic acid. The cysteine and sulphite reductones were estimated and found to be too small in amount to affect the conclusions drawn. Reductic acids were assumed to be absent (10). Dihydroxymaleic acid also appeared to be absent. There remained the possibility that hydroxytetronic acid might account in part for our results, but the close agreement between biological and chemical tests for ascorbic acid found by others (4, 10) suggests that our results were due to real changes in ascorbic acid.

The highly significant negative relationship between nitrate supply and ascorbic acid concentration was not unexpected (6). This nitrate effect was independent of molybdenum supply, however, and there is, therefore, no reason to suggest the existence of any direct relationship between ascorbic acid and nitrate reduction mediated by molybdenum.

Another possibility raised by the earlier observations (6), namely, whether the equilibrium between oxidation-reduction systems involving ascorbic acid and dehydroascorbic acid is directly affected by molybdenum status, merits discussion. Molybdenum supply evidently affected the ratio of the two compounds, as shown in Fig. 7, but in a complex manner. Thus changes in the ratio with changes in molybdenum supply over the range between 0·000005 and approximately 0·005–0·05 p.p.m. molybdenum were due to relatively large increases in ascorbic acid concentration accompanied mainly by negligible changes in dehydroascorbic acid concentration. Opposite and small changes in dehydroascorbic acid occurred only at 77 days growth. Over the range of the higher molybdenum levels from about 0·05 or 0·48 p.p.m. to 19·2 p.p.m. Mo the changes in the ascorbic ratio were due mainly to increases in dehydroascorbic acid without comparable changes in the ascorbic acid concentration. The results do not indicate any *direct* effect of molybdenum on the equilibrium between oxidation-reduction systems involving ascorbic and dehydroascorbic acids. Further discussion on this point will be deferred until additional evidence regarding the probable mechanisms involved is available.

The relationship of ascorbic acid concentration to chlorophyll content merits comment. It had been found (6) that molybdenum injection resulted in an increase in ascorbic acid before fresh chlorophyll production could be detected. The data for chlorophyll obtained in the present experiment at 55 days show (Figs. 1 and 2), however, between 0·000005 and 0·0005 p.p.m. Mo, certain changes in chlorophyll which are parallel with those for ascorbic acid. At other times such correspondence is not evident. Effects of increased nitrate supply on chlorophyll and on ascorbic acid content are opposite. The marked depressions in chlorophyll produced by high molybdenum supplies are not accompanied by similar decreases in ascorbic acid. The chlorophyll content in young leaves of plants in the low nitrate series (Fig. 2) remained relatively constant, while ascorbic acid concentration in similar leaves increased with increased molybdenum supply (Fig. 4).

Further discussion of the role of molybdenum in ascorbic acid production is deferred to subsequent papers in which the relationships between ascorbic acid concentration and sugars as affected by molybdenum supply and different sources of nitrogen will be described. The effects of molybdenum on the content of some possible precursors of ascorbic acid recently identified in plants (7, 8, 11, 12) merit investigation.

SUMMARY.

1. Cauliflower plants were grown in sand cultures with low and high nitrate supply and with 8 levels of molybdenum.

2. Molybdenum deficiency below 0·005 p.p.m. resulted in marked decreases in chlorophyll content in mature leaves.

Chlorophyll in young leaves was less affected by molybdenum status, and the effect was not appreciable at the low nitrate level.

3. Ascorbic acid concentration in leaves at several stages of growth increased with increasing molybdenum level up to 0·0005 p.p.m., and a concentration of 0·00005 p.p.m. produced a readily observed effect in older leaves.

4. Ascorbic acid concentration in stems was less than in leaves but showed similar variation. Curds and roots contained very little ascorbic acid.

5. High nitrate treatment usually resulted in a decreased ascorbic acid content.

6. Although there was a superficial correspondence between ascorbic acid and chlorophyll content there were several divergent effects. Neither chlorophyll content nor growth was thought to be a limiting factor for ascorbic acid content.

7. The dehydroascorbic acid : ascorbic acid ratio was a minimum at intermediate molybdenum levels, but the increases in the ratios at low and high molybdenum levels occurred for mainly different reasons.

8. Possible confusion or interference by cysteine reductones, reductic acids, dehydroxymaleic acid and hydroxytetronic acid are discussed. It is concluded that all but the last named may be excluded, and that the results probably reflected changes in true ascorbic acid.

ACKNOWLEDGMENTS.

The provision of an Overseas Research Studentship by the U.P. Government, India, is gratefully acknowledged by one of us (S.C.A.), whilst on 2 years study leave from the University of Lucknow.

We wish to thank Miss R. A. Paget for analytical assistance.

REFERENCES.

(1) *Agarwala, S. C.*, and *Hewitt, E. J.* (1954). Molybdenum as a plant nutrient. III. The interrelationships of molybdenum and nitrate supply in the growth and molybdenum content of cauliflower plants grown in sand culture. J. hort. Sci., **29**, 278–90.

(2) *Bolle-Jones, E. W.*, and *Notton, B. A.* (1953). The relative proportions of the chloroplast pigments as influenced by different levels of iron and potassium supply. Plant & Soil, **5,** 87.

(3) *Harris, L. J.*, and *Ray, S. N.* (1953). Vitamin C and the supra-renal cortex. III, with notes on a method for determining antiscorbutic activity by chemical measures. Biochem. J., **27,** 308.

(4) ——— and *Olliver, M.* (1942). Vitamin methods. III. The reliability of the method for estimating vitamin C by titration against 2 : 6 dichlorophenol indophenol. 1. Control tests with plant tissues. Biochem. J., **36,** 155.

(5) *Hewitt, E. J.* (1952). The use of sand and water culture methods in the study of plant nutrition. Tech. Commun. Bur. Hort. E. Malling, **22.**

(6) ———, *Agarwala, S. C.*, and *Jones, E. W.* (1950). Effect of molybdenum status on the ascorbic acid content of plants in sand culture. Nature, **166,** 1119.

(7) *Isherwood, F. A., Chen, Y. T.*, and *Mapson, L. W.* (1953). Synthesis of ascorbic acid in plants and animals. Nature, **171,** 348.

(8) ——— ——— ——— (1954). Synthesis of L. ascorbic acid in plants and animals. Biochem. J., **56,** 1.

(9) *Mapson, L. W.* (1951). Private communication.

(10) ——— (1943). Vitamin methods. VI. The estimation of ascorbic acid in the presence of reductones and allied substances. J. Soc. chem. Ind. *Trans.*, **62,** 223.

(11) ———, *Isherwood, F. A.*, and *Chen, Y. T.* (1954). Biological synthesis of L. ascorbic acid: the conversion of L. galactol γ lactone into L. ascorbic acid by plant mitochondria. Biochem. J., **56,** 21.

(12) *Nath, M. C., Chitale, R. P.*, and *Belavady, B.* (1952). Biosynthesis of vitamin C and a new precursor. Nature, **170,** 545.

(*Received* 15/2/54.)

COVER CROPS IN RELATION TO SOIL FERTILITY AND FRUIT TREE NUTRITION: THE EFFECT OF GRASS ON THE UPTAKE OF TOTAL AND FERTILIZER PHOSPHATE BY MALLING I ROOTSTOCKS

By C. BOULD, W. D. E. THOMAS and J. A. H. TOLHURST
Long Ashton Research Station, University of Bristol

It was shown by Bould (1) that the leaf phosphorus and potassium status of apple trees grown in grass under orchard conditions for 1–5 years was higher than that of leaves from trees growing under clean cultivation and annual cover crops, whereas the reverse was true for leaf nitrogen status. These findings were based on the percentage of the nutrients in the leaf dry matter. In the absence of information on the absolute amount of phosphorus in the whole tree it cannot be assumed that grass increased the uptake of phosphorus from the soil (inherent soil-P plus applied fertilizer-P). Since the total phosphorus content of a large tree cannot conveniently be determined it was decided to use apple rootstocks, growing in pots, to study the effect of grass and nitrogen supply on phosphorus uptake, fully realizing that pot culture conditions may differ considerably from those in the field. Two main experiments were carried out, the first in 1950 and the second in 1952. In the first experiment the rootstocks were grown with optimum supplies of nitrogen, whereas in the second experiment two fixed levels of nitrogen were used, both of which proved to be inadequate for optimum growth under grass cover.

The total phosphorus content of a plant, or any of its organs, and the corresponding concentration in dry matter can be determined chemically, but if phosphate labelled with P^{32} is used as fertilizer, then radio-assay of the plant digest solution permits the determination in the digest of the phosphorus derived from the fertilizer (henceforth referred to as fertilizer phosphorus). The difference between this fraction (fertilizer P) and the total phosphorus in the plant is derived partly from the inherent soil-P and partly from the old rootstock. By using fertilizer phosphate labelled with P^{32} it is possible to determine whether grass has any selective influence on the source or derivation of phosphorus in addition to any effect it may have on total phosphate uptake.

The use of fertilizer labelled with radio-active phosphorus in this way is dependent on two assumptions, firstly that there are no radiation effects on plant growth due to the tracer, and secondly that isotopic exchange between fertilizer phosphate and soil phosphate does not give rise to erroneous values. It is unlikely that radiation effects, sufficient to invalidate the results, occurred in these experiments. By using tracer at more than one level we were able to examine statistically any possible differences due to tracer and in no instance was tracer effect significant.

The importance of isotopic exchange in the interpretation of fertilizer uptake studies from soil is still not established. It may give rise to misleading data if the changes which occur to the fertilizer phosphate after sorption by the soil lead to the formation of forms less available to the plant than the original fertilizer. Spinks and

Barber (10) maintain that isotopic exchange does not give rise to erroneous results. McAuliffe *et al.* (7) have shown that isotopic exchange reduces the specific activity of the fertilizer in solution (ratio of radio-active to inactive fractions) and may reduce the estimated value for the uptake of fertilizer phosphate by plants. Russell *et al.* (9) have examined the problem of isotopic exchange under laboratory conditions and conclude that the tracer technique, when applied to fertilizer uptake, may give results which are no more reliable than by the old method, which is based on the increase in the phosphorus content of plants induced by the application of fertilizer.

It is difficult, in the light of present knowledge, to assess the magnitude of the effect of isotopic exchange on the measurement of fertilizer uptake by the tracer method, but it is unlikely to have accounted for the apparent selective influence of grass on the source of derivation of phosphorus in the present experiments, since isotopic exchange is likely to have occurred to the same extent under both cultural systems.

Numerous investigators have studied the effect of organic matter on phosphate availability. Jensen (6) found that the solubility of soil phosphate was increased by the addition of green manure, and ascribed this, in part, to the action of inorganic salts present, and in part to the solvent action of the organic decomposition products. Swenson *et al.* (11) suggested that organic acids formed during decomposition may be responsible for increased phosphate availability. Co-ordination of the organic anions with Fe and Al to give complexes more stable than the basic Fe and Al phosphates could result in the release of phosphate to the soil solution. Under acid conditions these organic anions may also saturate the Fe and Al valencies and so prevent the formation of the relatively unavailable Fe and Al phosphates. Dalton *et al.* (4) showed that additions of phosphorus-free organic matter to soil increased the phosphate content of Ladino clover and corn plants. Collison (3) has also presented data from lysimeter experiments which showed that phosphorus equivalent to more than 100 lb. superphosphate per acre may be made available each year through the growth and decomposition of a cover crop.

Readily decomposable organic matter would thus appear to be as effective as phosphate fertilization in promoting plant growth and the utilization of soil phosphate.

Experimental.

Pot experiment 1.

In late January, 1950, Malling I rootstocks, of a uniform grade, were planted singly in 10-in. bitumenized clay pots, each pot containing 7,000 g. of moist soil (21·7 per cent. moisture). The soil was a composite sample taken from Plot 20, Long Ashton Experimental Plots. It was a silty clay loam, pH 7·7 with free calcium carbonate and on analysis was found to contain 0·025 per cent. citric-soluble P_2O_5 and a similar amount of exchangeable potassium.

The potted rootstocks were placed in a cold glasshouse till early April, when they were transferred to a heated glasshouse and pruned to two buds above soil level. Only one shoot was allowed to develop.

Treatments. In early May half of the pots were sown with S.23 perennial rye grass. The grass was allowed to grow until it was about 2 in. high. From then onwards it was cut to 1 in. above soil level at frequent intervals. The cuttings remained on the surface of the pots and decomposed *in situ*.

On 4th June all pots were given a nutrient solution containing

0·307 g. K_2SO_4 per pot=1 cwt. per acre.
0·921 g. $(NH_4)_2SO_4$ per pot=3 cwt. per acre.
0·614 g. $MgSO_4.7H_2O$ per pot=2 cwt. per acre.

The amounts were calculated on the basis that the top 8 in. of soil from one acre weighs 2 million pounds. Further supplies of nitrogen, as ammonium sulphate, were given at intervals throughout the growing season so that the leaf nitrogen supply to all rootstocks was adequate.

Labelled phosphorus in the chemical form of orthophosphate, containing 0·76 g. $NaH_2PO_42H_2O$/200 ml., was applied to each pot on 5th June. The first solution contained no added tracer, the second and third contained tracer levels of 50 and 150 microcuries (μc) P^{32} as orthophosphate per 200 ml. respectively. Two levels of tracer were used as a precaution to permit detection of radiation effects, should they occur (2). The pots stood in bitumenized clay saucers and were watered in the normal way using a watering can with a fine rose.

The complete treatments were as follows :

1. Clean cultivation+$NaH_2PO_42H_2O$ (0·76 g.)
2. Clean cultivation+$NaH_2PO_42H_2O$ (0·76 g.)+50 μc P^{32}
3. Clean cultivation+$NaH_2PO_42H_2O$ (0·76 g.)+150 μc P^{32}
4. Perennial rye grass+$NaH_2PO_42H_2O$ (0·76 g.)
5. Perennial rye grass+$NaH_2PO_42H_2O$ (0·76 g.)+50 μc P^{32}
6. Perennial rye grass+$NaH_2PO_42H_2O$ (0·76 g.)+150 μc P^{32}

The pots were arranged in 5 randomized blocks, giving 5 replicates of each treatment.

Growth and harvesting. The rootstocks made vigorous growth and showed no abnormal symptoms which might be attributed to radiation damage. Towards the end of the experiment a few of the older leaves showed symptoms of magnesium deficiency.

On 16th August the plants were harvested. The leaves were first removed and placed in weighed beakers. Most of the soil was then washed from the rootstock, after removal of the pot, by placing it in a wire basket and dipping in and out of water containing a detergent. The last traces of soil were washed off the roots by supporting the plant on a perforated zinc tray and directing a jet of water on to the roots.

The roots were then cut off and placed in weighed beakers. Finally the stem, including the small 2-year-old basal portion, was cut into small sections and placed in a separate weighed beaker. Each plant therefore was divided into three portions, leaves, stem and roots.

Chemical analysis and radio-assay. The plant parts were dried to constant weight at 105° C. Organic matter was destroyed by wet digestion using concentrated nitric and perchloric acids.

After removal of excess acid by heating on a hot plate, the solutions were diluted with distilled water and boiled to convert phosphoric acids to the ortho form. The solutions were filtered, the filter washed with dilute nitric acid and the filtrate made up to 100 ml. When each batch was complete, i.e. leaves, stems, roots, it was assayed and total phosphorus was then determined in the residual solution by the phosphovanado-molybdate method of Hanson (5).

Radio-assay. Radioactive assay of the plant digests was carried out by solution counting using the M6 tube (12). Radio-active decay and any normal counter fluctuations were allowed for by assaying the corresponding stock solution after every two plant-digest solutions. A statistical precision of counting rather better than 98 per cent. was aimed at by counting for a sufficiently long time.

Pot experiment 2.

This experiment was designed to determine the effect of grass on the total phosphorus content and the fertilizer phosphorus uptake of apple rootstocks in the presence of two levels of added nitrogen and three levels of tracer. The second level of nitrogen (N_2) was double that of the first (N_1) but was given in two equal amounts on separate occasions, 5th May and 4th June respectively. The two rates of nitrogen corresponded to 3 and 6 cwt. per acre of ammonium sulphate.

The general technique and management was the same as in the previous experiment except that smaller pots were used, holding 4,560 g. of dry soil. The soil was similar to that used previously, but a small percentage of coarse grit was added to improve drainage.

Malling I rootstocks were planted on 6th March, and pruned to two buds later in the month. One half of the pots were sown with perennial rye grass on 22nd April. The rootstocks were carefully graded for size prior to the addition of radio-active phosphorus, and only those showing a uniform amount of new growth were used.

A nutrient solution containing potassium and magnesium sulphates, at similar rates to the first experiment, was given to each pot at the end of April.

Three stock solutions were again used, identical with those in Experiment 1 except that the lower tracer level was increased from 50 to 75 μc P^{32} per pot. In each case the phosphate was applied in 200 ml. aqueous solution to the surface of each pot on 1st May.

The complete treatments were :

1. Clean+N_1+$NaH_2PO_42H_2O$ (0·76 g.)
2. Clean+N_2+$NaH_2PO_42H_2O$ (0·76 g.)
3. Clean+N_1+$NaH_2PO_42H_2O$ (0·76 g.)+75 μc P^{32}
4. Clean+N_2+$NaH_2PO_42H_2O$ (0·76 g.)+75 μc P^{32}
5. Clean+N_1+$NaH_2PO_42H_2O$ (0·76 g.)+150 μc P^{32}
6. Clean+N_2+$NaH_2PO_42H_2O$ (0·76 g.)+150 μc P^{32}
7. Grass+N_1+$NaH_2PO_42H_2O$ (0·76 g.)
8. Grass+N_2+$NaH_2PO_42H_2O$ (0·76 g.)
9. Grass+N_1+$NaH_2PO_42H_2O$ (0·76 g.)+75 μc P^{32}
10. Grass+N_2+$NaH_2PO_42H_2O$ (0·76 g.)+75 μc P^{32}
11. Grass+N_1+$NaH_2PO_42H_2O$ (0·76 g.)+150 μc P^{32}
12. Grass+N_2+$NaH_2PO_42H_2O$ (0·76 g.)+150 μc P^{32}

The pots were arranged in 5 randomized blocks, giving 5 replications of each treatment.

Growth and harvesting. The plants made good growth until the beginning of June, when rootstocks under grass treatment showed signs of nitrogen deficiency. The second application of nitrogen was given to N_2 pots on 4th June. There was a temporary response to this additional nitrogen, but by the end of June all rootstocks under grass treatment were nitrogen deficient and growth was restricted. All plants

were harvested on 2nd and 3rd July. They were divided into leaves, stems, and roots, and treated as described in Experiment 1.

Table I.

Pot experiment 1. The effect of grass on the dry matter production of Malling I rootstocks in the presence of adequate nitrogen. Means of 15 pots.

	Clean	Grass	Remarks
	Dry matter g.	Dry matter g.	
Leaves	9·92	9·03	N.S.
Stems	16·98	15·75	N.S.
Roots	4·34	3·88	N.S.
Whole plant	31·24	28·66	N.S.

Results.

Pot experiment 1.

The effect of grass on the dry matter of leaves, stems and roots is shown in Table I. In the presence of adequate supplies of nitrogen, grass had no significant effect on dry matter production.

The effect of treatments on the fertilizer-P and total-P content of leaves, stems and roots is shown in Table II. Grass had a significant positive effect, at the 5 per cent. level of probability, on the fertilizer-P content of leaves, stems and whole plant but not of roots. Grass had no significant effect on the total-P content of any of the plant parts or of the whole plant.

Grass had no significant effect on the percentage of total-P in leaf dry matter. (See Table V.)

Table II.

Pot experiment 1. The effect of grass on the fertilizer-P and total-P contents of Malling I rootstocks in the presence of adequate nitrogen. Means of 15 pots.

		Clean	Grass	S.E. Mean	Sig. diff.		Remarks
		mgm. P	mgm. P		P=0·05*	P=0·01**	
Leaves	Fert. P ..	2·47	3·31	0·205	0·63	0·89	* Grass>Clean
	Total P ..	17·66	16·45	—	—	—	N.S.
Stems	Fert. P ..	2·32	3·21	0·279	0·86	1·21	* Grass>Clean
	Total P	17·41	16·06	—	—	—	N.S.
Roots	Fert. P ..	1·07	1·54	0·409	1·26	—	N.S.
	Total P ..	8·56	8·14	—	—	—	N.S.
Whole plant	Fert. P ..	5·86	8·06	0·588	1·81	2·54	* Grass>Clean
	Total P ..	43·63	40·65	—	—	—	N.S.

Pot experiment 2.

The effect of treatments on dry matter and phosphorus uptake are shown in Tables III and IV. For leaves, stems, roots and whole plant, dry matter production

was much greater under clean cultivation than under grass treatment. Additional nitrogen increased leaf dry matter but decreased root dry matter.

Grass decreased the fertilizer and total phosphorus content of leaves, stems and whole plant but had no significant effect on the phosphorus content of roots. Additional nitrogen increased the total phosphorus content of leaves but decreased the total phosphorus content of roots. This is in keeping with the effect on dry matter.

The effect of treatments on total-P expressed as a percentage of leaf dry matter is shown in Table V. Treatments had no significant effect on percentage P in leaf dry matter.

There was no significant effect due to tracer level on any of the functions investigated.

TABLE III.

Experiment 2. The effect of grass at two levels of nitrogen on the dry matter production of leaves, stems and roots of Malling I apple rootstocks. Mean values per pot.

	Nitrogen level	Clean	Grass	S.E.	Sig. diff.		Remarks
		Dry matter g.	Dry matter g.		P=0·05*	P=0·01**	
Leaves	N_2	6·88	4·19				
	N_1	6·61	2·96				* High N>Low N
	Mean N_1+N_2	6·75	3·58	0·671	1·92	2·57	** Clean>Grass
Stems	N_2	14·10	10·35.				
	N_1	15·13	8·99				
	Mean N_1+N_2	14·62	9·67	0·489	1·40	1·87	** Clean>Grass
Roots	N_2	4·61	3·38				
	N_1	5·70	3·96				* Low N>High N
	Mean N_1+N_2	5·16	3·67	0·228	0·65	0·87	** Clean>Grass
Whole plant	N_2	25·60	17·92				
	N_1	27·44	15·91				
	Mean N_1+N_2	26·52	16·92	0·849	2·43	3·25	** Clean>Grass

DISCUSSION.

The results of these two pot experiments show that the effect of grass on the dry matter production and phosphate uptake by apple rootstocks is related to the nitrogen supply, when other nutrients are present in adequate amounts. In the presence of ample nitrogen, grass had no deleterious effect on growth, as measured by dry matter production. This is contrary to the findings of Pickering (8), who suggested that grass produced toxic substances which interfered with the tree's metabolism.

Grass, in the presence of adequate supplies of nitrogen, had a significant positive effect on the uptake of fertilizer phosphorus ; the mean increase, compared with clean cultivation, amounted to approximately 37 per cent. This effect may be due to the decomposition products of grass combining with active iron and aluminium compounds in the soil and reducing fixation of fertilizer phosphate, or to the initial uptake by the grass of fertilizer phosphate and its subsequent release. The grass cuttings, on decomposition and de-phosphorylation of organic phosphorus compounds,

Table IV.

Experiment 2. The effect of grass at two levels of nitrogen on the fertilizer and total phosphorus uptake of leaves, stems and roots of Malling I apple rootstocks. Mean values per pot.

		Clean	Grass	S.E.	Sig. diff.		Remarks
		mgm. P	mgm. P	Mean	P=0·05*	P=0·01**	
Leaves	*Fert. P*						
	N_2	2·25	1·18				
	N_1	1·96	0·90				
	Mean N_1+N_2	2·10	1·04	0·153	0·45	0·61	** Clean>Grass
Leaves	*Total P*						
	N_2	15·86	10·24				
	N_1	14·98	7·05				* High N>Low N
	Mean N_1+N_2	15·41	8·64	0·592	1·69	2·26	** Clean>Grass
Stems	*Fert. P*						
	N_2	1·86	0·90				
	N_1	1·52	0·67				
	Mean N_1+N_2	1·69	0·78	0·128	0·38	0·52	** Clean>Grass
Stems	*Total P*						
	N_2	11·17	8·13				
	N_1	11·12	6·62				
	Mean N_1+N_2	11·14	7·38	0·566	1·62	2·16	** Clean>Grass
Roots	*Fert. P*						
	N_2	1·17	0·88				
	N_1	1·26	1·32				
	Mean N_1+N_2	1·22	1·10	—	—	—	N.S.
Roots	*Total P*						
	N_2	7·30	6·94				
	N_1	9·04	8·83				** Low N>High N
	Mean N_1+N_2	8·17	7·88	0·45	1·29	1·72	N.S.
Whole plant	*Fert. P*						
	N_2	5·28	2·95				
	N_1	4·74	2·88				
	Mean N_1+N_2	5·01	2·92	0·365	1·08	1·47	** Clean>Grass
Whole plant	*Total P*						
	N_2	34·30	25·31				
	N_1	35·15	22·50				
	Mean N_1+N_2	34·73	23·91	1·304	3·73	4·99	** Clean>Grass

Table V.

The effect of grass on the mean phosphorus content of Malling I rootstock leaves. Phosphorus expressed as a percentage of leaf dry matter.

	Nitrogen level	% P in leaf dry matter		Remarks
		Clean cultivation	Grass	
Experiment 1 ..	High	0·178	0·181	N.S.
Experiment 2 ..	N_1	0·228	0·241	N.S.
,, ..	N_2	0·270	0·249	N.S.
,, ..	Mean N_1+N_2	0·249	0·245	N.S.

would liberate available phosphate, thus extending the period during which absorption by the apple rootstocks of fertilizer phosphate could take place.

The total phosphorus content of the rootstocks in the presence of adequate supplies of nitrogen was unaffected by grass, as was the total phosphorus concentration of the leaf when expressed as a percentage of dry matter.

The effect of grass on dry matter production and phosphorus uptake in the absence of adequate supplies of nitrogen was quite different. Under these conditions grass reduced dry matter of roots, stems and leaves and the fertilizer-P and total phosphorus of leaves, stems and whole plant. The effect on total P of roots was not significant. Additional nitrogen increased the total phosphorus content of leaves, had no significant effect on stems, but reduced the total phosphorus content of roots. This nitrogen effect was more pronounced under grass treatment than in the absence of cover. Treatments had no significant effect on the concentration of phosphorus in leaf dry matter. This is contrary to the long-term grass effects observed under field conditions. In the orchard experiment, grass reduced the nitrogen status of the leaf and, over a period of years, steadily increased the percentage leaf phosphorus to luxury consumption level. No data are available on leaf nitrogen levels in the pot experiments.

The duration of the pot experiments was necessarily short, being limited by the half life of P^{32} and the amount applied. It is unfair, therefore, to compare critically the short-term effects obtained under pot conditions with the cumulative effects of several years under grass orchard conditions. The short-term effect of grass, as determined by pot experiments, is on fertilizer-P uptake rather than on mobilization of soil-P.

SUMMARY.

1. The effect of perennial rye grass versus clean cultivation on the fertilizer-P and total phosphorus uptake by Malling I apple rootstocks has been studied by pot experiments using P^{32}.

2. In the presence of adequate supplies of nitrogen and other nutrients, grass, when cut frequently and the cuttings allowed to decompose *in situ*, increased the uptake of fertilizer phosphorus by 37 per cent. Total phosphorus content was not affected.

3. In the absence of adequate supplies of nitrogen, grass reduced dry matter, fertilizer-P uptake and total phosphorus content.

4. Grass had no effect on the percentage of total phosphorus in leaf dry matter. This is contrary to the findings of long-term grass orchard experiments.

5. Tracer level had no effect on any of the functions investigated.

REFERENCES.

(1) *Bould, C.* (1950). The influence of cultural practices on the nutrient uptake of apples. Transactions 4th International Congr. Soil Sci., Amsterdam, **1**, 262.

(2) ———, *Nicholas, D. J. D.*, and *Thomas, W. D. E.* (1951). Radiation effects in plant nutrition experiments with phosphorus-32. Nature, **167**, 140.

(3) *Collison, R. C.* (1937). Potash and phosphorus in relation to organic matter in New York orchards. N.Y. State agric. Exp. Sta. Bull. **679**.

(4) *Dalton, J. D., Russell, G. C.*, and *Sieling, D. H.* (1952). Effect of organic matter on phosphate availability. Soil Sci., **73,** 173.

(5) *Hanson, W. C.* (1950). The photometric determination of phosphorus in fertilizers using the phosphovanado-molybdate complex. J. Sci. of Food and Agric., **1**, 172.

(6) *Jensen, C. A.* (1917). Effect of decomposing organic matter on the solubility of certain inorganic constituents of the soil. J. agric. Res., **9,** 253.

(7) *McAuliffe, C., Peech, M.*, and *Bradfield, R.* (1949). Utilization by plants of phosphorus in farm manure : II. Availability to plants of organic and inorganic forms of phosphorus in sheep manure. Soil Sci., **68,** 185.

(8) *Pickering, S.* (1927). The scientific work of the late Spencer Pickering, F.R.S., by Lowry and Russell. Harrison & Sons Ltd., London.

(9) *Russell, R. Scott, Rickson, J. B.*, and *Adams, S. N.* (1954). Isotopic equilibria between phosphates in soil and their significance in the assessment of fertility by tracer methods. J. Soil Sci., **5,** 85.

(10) *Spinks, J. W. T.*, and *Barber, S. A.* (1947). Study of fertilizer uptake using radioactive phosphorus. Sci. Agric., **27,** 145.

(11) *Swenson, R. M., Cole, C. V.*, and *Sieling, D. H.* (1949). Fixation of phosphate by iron and aluminium and replacement by organic and inorganic ions. Soil Sci., **67,** 3.

(12) *Veall, N.* (1948). A Geiger Muller counter for measuring the Beta-ray activity of liquids, and its application to medical tracer experiments. Brit. J. Radiol., **21,** 347.

(*Received* 25/2/54.)

REVIEWS

PLANT GROWTH SUBSTANCES. By Professor L. J. Audus, M.A., Ph.D. (London: Leonard Hill Ltd. 1953. Pp. 366+v-xix and Glossary 367-75, Appendices 377-414, Bibliography 415-38, Indices 439-65, and 53 illustrations. Price 42s.)

Although much important work on plant growth substances has been done in this country, summarizing the subject as a whole has mainly been left to workers elsewhere. It is therefore particularly gratifying that this latest attempt to review the field should have resulted in such an excellent book as this by Professor Audus.

He is himself engaged in this work and it is all the more to his credit that he has managed to " stand back " from it sufficiently to be able to " see the wood *and* the trees ", and to be able both to present the general scene and to describe the often complicated detail equally clearly in simple and unpretentious language.

As stated in the introduction the author has not restricted the book to a description of the established practical uses for growth substances and their relation to the physiology of the plant, but has also included aspects of theoretical interest. By boldly casting his net wide and drawing in such diverse catches as stereochemistry, photoperiodism, leaf-form and the sexual hormones of the water-mould *Achlya*—the first examples of many to come to mind—the author has successfully postponed the day when the book will be out of date, a fate which so rapidly overtakes many modern textbooks.

For the same reason there is no need for the apology in the introduction (vii) even to the " exacting specialist " ; it is just he who should most benefit by being made to take " a view of the broadest possible horizon " (vi), and this book should help, for example, the worker on fruit-drop control by growth substances to remember that these same compounds may also be important in tissue-culture studies and pineapple production.

Another valuable attribute of the volume is that growth substances are not presented as the " universal panacea ", an often-encountered approach to the subject which does more harm than good to the development of these substances for practical uses ; similarly, it is comforting to see words of warning given periodically against the use of certain substances on edible crops before they have been shown to be entirely innocuous to man.

The first three chapters introduce the nature of plant growth, auxins and their chemistry, the last, among other things, dealing fairly with the vexed question of the existence of " Auxins A and B ". The next four cover the stimulating effects of auxins (here used to include both natural and synthetic substances) ; Chapters 8 and 9 treat the inhibition of growth by auxins, and Chapters 10 and 11 discuss their use in controlling abscission and for miscellaneous purposes. The effect of growth substances on respiration has not been touched on at all. The remaining chapters (12-15) are devoted to other hormone systems in the plant and include a consideration of vitamins and growth inhibitors and their importance in the growth and development, not only of angiosperms but of the " lower " plants as well.

A glossary and five interesting appendices follow, and a bibliography of over 700 references ; no doubt considerations of space led to the omission of the titles of

individual papers, but their presence would have made it even more useful. Comprehensive subject and author indices complete the book.

The illustrations are well chosen and well reproduced, and some (such as Figs. 17 and 31) are ingenious presentations of general trends shown in data which are otherwise very difficult to assimilate. Fig. 29 is an exception : it is hard to grasp the significance of the photograph in the absence of an untreated seedling ; while Fig. 9, otherwise a very neat summary of four assay methods for auxin, is perhaps rather misleading in the detail of the concentration response curves shown.

These, however, are minor criticisms which detract little from an excellent work which should be of interest and value to layman and " initiate " alike.

H.W.B.B.

THE MEASUREMENT OF PLANT CLIMATE. By S. A. Searle. (Chichester : Chichester Press Ltd. 1953. Pp. 36, illus. Price 4s. 6d.)

The author gives an account of the factors affecting plant climate and describes a " plant climate thermometer ", which is virtually a soil thermometer showing temperature deviation from the average mean soil temperature.

The climatic index proposed for use is the mean temperature of the soil at 12 in. depth under grass. The temperature deviation from average at any time for a particular location is the suggested criterion for interpreting the effects of climate on plant growth.

In this reviewer's opinion, far too little is known to evaluate the importance of soil temperature as a factor in the shoot growth of plants, and the consideration of the author that the instrument " virtually integrates all the climatic factors " needs to be critically examined.

A useful series of maps is presented showing mean temperatures at 12 in. depth under grass for each month of the year for the British Isles.

J.E.G.

SOILLESS CULTURE. By T. Saunby. (London : Collingridge Ltd. 1954. Pp. 104, illus. Price 12s. 6d. net.)

This is essentially a practical book for the man who wishes to try soilless cultivation for crop production. Only sufficient nutritional physiology is given to enable a grower to compound and handle the necessary nutrient solutions. Within these limits, the notes given are succinct and informative. Full details of construction of different types of bed are given, and the author contributes an original method for application of the nutrient solution, which is simple and effective, as he has proved in commercial practice. Adequate details are provided for the raising and management of tomatoes, carnations and pot plants. A useful and accurate handbook.

R.H.S.

WINE GROWING IN ENGLAND. By G. Ordish. (London : Hart-Davis. 1953. Pp. 128, bibl. 60, illus. Price 7s. 6d.)

This small book is the production of one who believes that the best reason for drinking wine is because one likes it. None, moreover, will disagree with his statement that, unless one makes one's own wine, daily wine drinking in Britain is expensive.

He himself lived in France for some years, where presumably he became addicted

to the habit. Later coming to live in Kent, he found the climate not unlike that of Champagne. Very slight further investigation led him to plant vines. " Some good wine and this book are the results." The present reviewer considers them most laudable.

In these few pages the reader will find a clear and concise account of methods first of planting and cultivating his vines, and secondly of converting their products into a light, claret-like wine or a white wine resembling still champagne. There is no suggestion of searching Europe or elsewhere for hardy exotics, but while the author notes that claims are put forward on behalf of a number of other vines, he finds that Brandt, a hybrid of a Canadian and European vine, followed closely by Gamay Hâtif, both with black grapes, will best answer the purpose for red wine, while for white he suggests that Madeleine Royal and Meslier Précoce should be tried. Briefly explaining the main principles underlying wine-making, he gives ample practical instructions on how to proceed and discusses the apparatus necessary. While essentially he writes for the householder who wants to " grow " his own wine, he devotes one chapter to the consideration of commercial production.

This is in the reviewer's opinion the simplest and most satisfactory manual so far produced for the would-be amateur vine grower in England. Note also its price.

D.A.

PLANT LIFE IN MALAYA. By R. E. Holttum. (London, New York, Toronto : Longmans, Green & Co. 1954. Pp. 254, illus. Price 18s.)

Botanically, Malaya is one of the richest areas of the world. This statement is true whether its basis be floristic or vegetational. There has been an enormous development of genera and species, many endemic, and the lush growth of tall forest can be correlated with the almost optimal environmental conditions, particularly of temperature and humidity, throughout the year. Professor Holttum, from his long personal experiences in Malaya as a professional botanist, is well qualified to describe various aspects of the plant life of the Peninsula. This he has done in what are in the main a series of more or less independent essays dealing either with a particular systematic group of plants or with some life-form or other grouping. Forest is the characteristic major community of Malaya. The tall evergreen forest covers the whole of the lowlands up to about 4,000 ft., except where it has been destroyed or modified by human interference. In this forest, dipterocarps, of many kinds, account for a large proportion of the tallest trees, which control the general organization of the whole community. Smaller trees are very varied. Nearer the ground are shrubs, small palms, gingers, ferns, herbaceous plants, and seedlings and young plants of many kinds. Climbers, especially woody climbers or lianes and epiphytes, are exceedingly numerous. Above 4,000 ft., dipterocarps die out and the mountain forest replaces the lowland forest. In this mountain forest members of the oak and laurel families are conspicuous and the ground vegetation is often richer than in the lowland forest. In the various chapters both structural and physiological accounts are given of many of the more important plants of the Malayan forest. Professor Holttum has himself specialized on the ferns and their allies and on the orchids. His chapters on these groups have, therefore, a particular value. Several chapters deal with the vegetative life of Malayan plants, such as the structure and behaviour of roots and stems and the many forms of vegetative propagation. Reproduction, with the sequence of flowers, fruits, and seeds, under tropical conditions

is considered at some length. Yams (and other tubers), bananas, and grasses are given separate essays. Studies of life-form groups include those on climbing plants, parasites and saprophytes, and water plants. The close interaction of plants and animals is illustrated not only by the part played by animals in pollination and dispersal, but also by the many linkages between plants and ants.

The book is nicely produced. The frontispiece, " In the forest in the Bertam valley, Cameron Highlands, Malaya (4,700 feet altitude) ", gives a vivid picture of the density and variety of a Malayan mountain forest. In addition, there are many full-page line drawings, prepared to illustrate the text. A list of botanical equivalents of Malay and English plant names is useful in reading the book, assuming that the reader is sufficiently acquainted with systematic botany to visualize the plants by their Latin names.

It is stated that the book is primarily intended for residents in Malaya, especially for teachers, senior students in schools and first year university students. It is, however, not a textbook in the ordinary sense of the term, and can be read with interest and advantage by all who wish to learn something of the great wealth of plant life in a tropical country and one that has been " much in the news " in recent years. W.B.T.

THE CALCULATION OF IRRIGATION NEED. Ministry of Agriculture Technical Bulletin No. 4. (London : H.M. Stationery Office. 1954. Pp. 38, illus. Price 2s.)

This bulletin has been published to supplement the Ministry's Bulletin No. 138, " Irrigation ", which has recently been completely revised.

It describes in a complete and reasonably concise form the problems of controlled irrigation, and the available solutions of these problems based on the calculation of potential transpiration from weather data.

The bulletin will serve as an invaluable handbook for all concerned in the irrigation of field crops. A section is included dealing with water requirements of plants under glass, but at the present time direct measurement of soil moisture seems still the most precise method of assessing the irrigation need of glasshouse crops.

The practical use of the methods of calculating irrigation need is well explained, and examples are given making it relatively easy for anyone to use the information provided without complicated formulae and with only a gauge to measure rainfall.

The bulletin has a particular use for those who doubt whether irrigation is necessary in their own localities. Maps have been prepared showing the probable irrigation need throughout England and Wales. J.E.G.

INSECTICIDES AND COLONIAL AGRICULTURAL DEVELOPMENT. Edited by T. Wallace and J. T. Martin. (London : Butterworths. 1954. Pp. 169, illus. Price 30s.)

This useful volume records the Proceedings of the Sixth Symposium of the Colston Research Society held at the University of Bristol in 1953. The policy, aims and achievements of the Society, given in a foreword by Sir Havergal Downes-Shaw, reveal the extent to which these annual symposia are leading to the advancement and stimulation of knowledge in specific fields of endeavour, and it is regrettable that more such bodies do not exist.

A vast amount of literature on insecticides has arisen from the big advances made in this field in recent years. Yet, in spite of this and the fact that losses caused by insect pests of crops grown in the Colonial territories may be as high as £100 million annually, there had been no previous serious attempt to review what has already been accomplished and what progress is being made in the use of insecticides in these regions. The Sixth Colston Symposium set out to satisfy this need, and there is no doubt whatever that it has done so in a most successful manner.

The programme as a whole was well balanced, allowing full opportunity to entomologists from different colonies to state and discuss their problems and for leading workers in this country to deal with other aspects of insect pest control. The broad treatment adopted by most of the speakers is to be commended, and although the Symposium was concerned with insecticides, other non-chemical methods of crop protection were not forgotten. All the contributors delivered papers of a high standard. Together they provide a wealth of information, are very readable and reflect the enthusiasm of the writers. The paper by Fennah, however, seems to strike a somewhat pessimistic note which may be personal or may indicate a different attitude towards farming in the West Indies as compared with Africa. Most of the authors rightly stress the need for insecticides of low human toxicity which can be applied cheaply and simply by native peasant farmers. The conflict between this latter requirement and the need for efficient application is ably considered by Kearns, whose paper as a whole on spraying technique and machinery is outstanding. The widespread use of known potent insecticides before an adequate field study of the pest has been made, is deprecated by several speakers. A plea for careful studies of the effects of insecticides on the ecological balance is made by Way, and McKinlay stresses the importance of investigating the relationship between pest attack and loss of yield before using insecticides on a wide scale. Both McKinlay and Swaine emphasize the desirability of investigating the extent to which damage is caused by insect pests under the conditions of African native agriculture. Most of these views are well expressed in a statement made by Jepson that " entomological study at the site of action is the key to the proper use of insecticides ".

An excellent paper by Hall, at the beginning of the Symposium, deals with the value of the crops produced in the Colonies, estimates of the losses due to pests and how far the proper use of insecticides might help to increase agricultural production in these territories. He stresses the need for basic research, for more funds and for more workers, especially entomologists, and the ideas he develops on the organization of plant protection in the Colonies deserve careful consideration. The case for more fundamental research is also dealt with by Symes. Munro, discussing crop losses caused by insect pests during storage and transit, pleads for a new attitude towards the training of technologists with practical knowledge of fumigants and other insecticides. The prominence of DDT, BHC and the other chlorinated insecticides is notable in all the discussions, and it is obvious that their persistence and stability under tropical conditions require further study.

Three papers are included on the control of animal parasites, and another deals with some of the problems of insecticide manufacturers. A contribution from non-commercial chemical research might, with advantage, have been included, and the importance of such factors as insecticidal formulation could have been given greater attention.

The editors and publishers are to be congratulated on the standard of presenta-

tion reached in this volume. Indeed, the very high quality of the production makes one wonder if it could not have been possible to produce a lasting volume at somewhat lower cost. This book is nevertheless one which all who are interested in insecticides or in Colonial agriculture should possess. R.L.W.

THE DESIGN AND ANALYSIS OF EXPERIMENT. By M. H. Quenouille. (London : Chas. Griffin & Co. Ltd. 1953. Pp. 356. Price 36s.)

The critics who maintain that all books on statistics are the same except for the order of the chapters should read this one, for it is a most distinctive production, the differences in the main being for the better. It is not clear to what class of reader the book is addressed, but it should be stated right away that it will not suit the beginner ; for one thing, words are sometimes used in some undefined sense personal to the author (the word " experiment " in the title is an example of this), and for another, the quality is uneven, some subjects such as missing plot technique being dealt with inadequately, while others such as the effect of the failure of whole treatments are examined with enthusiasm and much detail. Also, the extensive bibliography is rather queer, ending as it virtually does in 1950 and having no perceptible connection with the text. On the other hand, for anyone who has already had some experience, this is a most sprightly and stimulating publication, for the outlook is original, the examples apt and the whole text charged with that common sense that comes from actual contact with experiments as opposed to lecturing on the mathematical theory of statistics.

One especially admirable feature is the emphasis on the need to examine the raw data as a preliminary to analysis. One delightful example is afforded by a trial on peas in which four levels of a fertilizer, including none at all, were applied using three methods of placement, and the experimenters had assumed that no fertilizer would necessarily give the same result whatever the placement method. As Mr. Quenouille points out, however, their own data suggest that this is not so, the disturbance of the soil itself having an effect on germination. Incidentally, he does not point out the moral that the trial could usefully have included a genuine *nil* treatment, but this omission is not characteristic. His comments on the examples are full and informed.

Also of especial value is the section on " long term policy ", which starts off on its stated subject, but soon develops into an exceedingly valuable discussion on the problems of designing and analysing groups of experiments, whether carried out at one time or in sequence, this being one of the most useful parts of the book. Also, there are some good methods of examining the residual effects of treatments as well as immediate ones, a comprehensive discussion of the uses of transformations, an ingenious and simple method of dealing with an experiment in which a treatment has been applied in error to the wrong plots and much else. Where the author is interested he writes clearly and with originality, and if he links these excellent isolated essays with passages that at times do little more than present a continuous façade and occasionally reveal a surprising gap, he will be readily forgiven. The reviewer does not know everything either, and it is a long time since he read a statistical book with so much enjoyment, or one from which he has learnt so much, or one more calculated to get him out of a rut, and he is grateful to Mr. Quenouille for the experience. S.C.P.

PUBLICATIONS RECEIVED.

AMATEUR GARDENING ANNUAL. A Preview of the Year's Work 1954. Edited by A. G. L. Hellyer. (London : W. H. & L. Collingridge Ltd. 1953. Pp. 136, illus. Price 5s.)

DISEASES AND PESTS ON HORTICULTURAL PLANTING MATERIAL. A Guide to their Recognition. Ministry of Agriculture and Fisheries. (London : H.M. Stationery Office, 1953. Pp. 38, illus. Price 6s.)

THE COMMERCIAL GROWER YEAR BOOK AND DIARY 1954. (London : Benn Brothers Ltd. 1953. Pp. 260, illus. Price 10s. 6d.)

THE FORTY-SIXTH ANNUAL REPORT OF THE GOVERNING BODY OF THE IMPERIAL COLLEGE OF SCIENCE AND TECHNOLOGY. (London. 1954. Pp. 55.)

THE YEAR'S VEGETABLES. WHEN TO SOW, GROW AND GATHER. By H. C. Davidson. (London : Fredk. Warne & Co. Ltd. 1954. Pp. 46, illus. Price 1s. 6d.)

VERSLAG VAN DE STICHTING " BOOM EN VRUCHT " TE OPHEUSDEN OVER DE JAREN 1951-1952 EN ENKELE VOORLOPIGE MEDEDELINGEN OVER 1953 EN VERSLAG VAN HET RIJKSTUINBOUWCONSULENTSCHAP TE KESTEREN OVER DE JAREN 1951-1952 EN ENKELE VOORLOPIGE MEDEDELINGEN OVER 1953. (Report of the " Tree and Fruit " Institute, Opheusden, for 1951-1952, with some preliminary observations for 1953 and Report of the extension and research work of the State Horticultural Advisory Service in Kesteren for 1951-1952 with some preliminary observations for 1953.) Pp. 151.

THE TULIP'S QUATER-CENTENARY. The Financial Times, 22nd April, 1954, p. 6.

INDEX

JOURNAL OF HORTICULTURAL SCIENCE, Vol. XXIX.

PAGE

Agarwala, S. C. and Hewitt, E. J. Molybdenum as a plant nutrient:
III. The interrelationships of molybdenum and nitrate supply in the growth and molybdenum content of cauliflower plants grown in sand culture 278
IV. The interrelationships of molybdenum and nitrate supply in chlorophyll and ascorbic acid fractions in cauliflower plants grown in sand culture 291

Apple:
Chemical composition of leaves of, in relation to nutritional treatment. (Eaves and Kelsall) 59
Effects of fruit thinning by the leaf count method on yield, size and biennial bearing of the apple Duchess Favourite. (Preston) 269
Experiments on the control of Brown Rot. (Byrde) 226
Influence of intermediate stem-piece upon the scion. (Thomas) 150
Insecticidal efficiency of DDT applied to foliage. (Satyanarayana) .. 112
Reinvigoration of trees by inarching. (Thompson, Roach and Preston) .. 175
Relation between rate of respiration of a fruit and its content of protein. (Hulme) 98
Respiration progress curves for Cox's Orange Pippin for consecutive seasons. (Hulme) 142

Banana:
Gros Michel, seed fertility of the, in Jamaica. (Shepherd) 1
Varietal identification in the Cavendish group of, (Simmonds) 81

Bolas, B. D. (Ruck and Bolas) 193

Book Reviews:
Gardening in warm climates. By D. A. Herbert 76
Growing fruit and vegetable crops. By T. J. Talbert 236
Insecticides and colonial agricultural development. Edited by T. Wallace and J. T. Martin 313
Obstbau Grundlagen, Anbau und Betrieb (3rd Ed.). By F. Hilkenbäumer 77
Perpetual flowering carnations. By R. J. Morton 72
Physiology of seeds. By W. Crocker and L. V. Barton 76
Plant anatomy. By Katherine Esau 75
Plant diseases. By F. T. Brooks 74
Plant growth substances. By Prof. L. J. Audus 310
Plant life in Malaya. By R. E. Holttum 312
Russian comfrey. By L. D. Hills 235
Science and fruit. Edited by T. Wallace and R. W. Marsh 153
Soilless culture. By T. Saunby 311
South Indian horticulture 235
Statistical science in agriculture. By D. J. Finney 154
Strawberry cultivation. By E. Hyams 78
Studies in British beechwoods. By J. M. B. Brown 72
The calculation of irrigation need. (H.M.S.O. publication) 313
The daffodil and tulip year book. (R.H.S.) 235
The design and analysis of experiment. By M. H. Quenouille 315
The fruit year book. (R.H.S.) 235
The geography of the flowering plants. By R. Good 73
The lily year book. (R.H.S.) 235
The measurement of plant climate. By S. A. Searle 311
The rhododendron and camellia year book. (R.H.S.) 235
Wine growing in England. By G. Ordish 311

PAGE

BOULD, C. and CATLOW, E. Manurial experiments with fruit. I. The effect of long-term manurial treatments on soil fertility and on the growth, yield and leaf nutrient status of strawberry, *var.* Climax 203

———, THOMAS, W. D. E. and TOLHURST, J. A. H. Cover crops in relation to soil fertility and fruit tree nutrition : The effect of grass on the uptake of total and fertilizer phosphate by Malling I rootstocks 301

BROWN ROT :
Of apples and plums. Experiments on the control of, (Byrde) 226

BUNT, A. C. Steam pressure in soil sterilization. I. In bins 89

BYRDE, R. J. W. Experiments on the control of Brown Rot of apples and plums. IV. A supplementary note on winter spraying 226

CALVERT, A. (Lawrence and Calvert) 157

CATLOW, E. (Bould and Catlow) 203

CHERRY :
Survey of virus diseases of, in England. (Posnette) 44

COVER CROPS :
In relation to soil fertility and fruit tree nutrition. (Bould, Thomas and Tolhurst) 301

CROWE, L. K. (Lewis and Crowe) 220

DAFFODIL :
Effects of deficiencies and excesses of some mineral nutrients on the growth of, (Hewitt and Miles) 237

EAVES, C. A. and KELSALL, A. Chemical composition of Cortland apple leaves in relation to nutritional treatment 59

FROST :
Resistance to, of raspberry, affected by maleic hydrazide. (Modlibowska and Ruxton) 184
Water-sprinkling as a measure against injury to fruit blossom. (Rogers, Modlibowska, Ruxton and Slater) 126

FRUIT THINNING :
Effects of, by the leaf count method, on yield, size and biennial bearing of the apple Duchess Favourite. (Preston) 269

GARNER, R. J. (Mosse and Garner) 12

HEWITT, E. J. (Agarwala and Hewitt) 278, 291

——— and MILES, PEGGY. The effects of deficiencies and excesses of some mineral nutrients on the growth of tulip and daffodil bulbs in sand culture 237

HUDSON, J. P. Propagation of plants by root cuttings. I. Regeneration of raspberry root cuttings 27

HULME, A. C. Studies on the maturity of apples. Respiration progress curves for Cox's Orange Pippin apples for a number of consecutive seasons .. 142

——— The relation between the rate of respiration of an apple fruit and its content of protein. II. The value of the relation immediately after picking and at the respiration-climacteric for several varieties of apples 98

KELSALL, A. (Eaves and Kelsall) 59

LAWRENCE, W. J. C. and CALVERT, A. The artificial illumination of seedlings .. 157

LEWIS, D. and CROWE, L. K. The induction of self-fertility in tree fruits 220

LIGHT :
Artificial, for seedling growth. (Lawrence and Calvert) 157

MILES, PEGGY. (Hewitt and Miles) 237

PAGE

MODLIBOWSKA, IRENA. (Rogers, Modlibowska, Ruxton and Slater) 126

——— and RUXTON, J. P. The effect of maleic hydrazide on the spring frost resistance of the Malling Exploit raspberry 184

MOLYBDENUM :
As a plant nutrient. (Agarwala and Hewitt) 278, 291

MONTGOMERY, NANCY. Damping-off of tomato by species of *Pythium* and its control by use of formalin dust 245

MOSSE, BARBARA and GARNER, R. J. Growth and structural changes induced in plum by an additional scion 12

PLUM :
Experiments on the control of Brown Rot. (Byrde) 226
Growth and structural changes induced in, by an additional scion. (Mosse and Garner) 12

POSNETTE, A. F. Virus diseases of cherry trees in England. I. Survey of diseases present 44

POTATO :
Effect of soil carbon dioxide on manganese uptake and growth of, (Ruck and Bolas) 193

PRESTON, A. P. Effects of fruit thinning by the leaf count method on yield, size and biennial bearing of the apple Duchess Favourite 269

———. (Thompson, Roach and Preston) 175

RASPBERRY :
Regeneration of root cuttings. (Hudson) 27
Spring frost resistance, effect of maleic hydrazide on, (Modlibowska and Ruxton) 184

ROACH, W. A. (Thompson, Roach and Preston) 175

ROBERTSON, MARGARET and WOOD, C. A. Studies in the development of the strawberry :
I. Flower-bud initiation and development in early- and late-formed runners in 1951 and 1952 104
II. Stolon production by first-year plants in 1952 231

ROGERS, W. S., MODLIBOWSKA, IRENA, RUXTON, J. P. and SLATER, C. H. W. Low temperature injury to fruit blossom. IV. Further experiments on water-sprinkling as an anti-frost measure 126

———. (Wilson and Rogers) 21

RUCK, H. C. and BOLAS, B. D. The effect of soil carbon dioxide on manganese uptake and growth of the potato 193

RUXTON, J. P. (Modlibowska and Ruxton) 184

———. (Rogers, Modlibowska, Ruxton and Slater) 126

SALTER, P. J. The effects of different water-regimes on the growth of plants under glass. I. Experiments with tomatoes (*Lycopersicum esculentum* Mill.) 258

SATYANARAYANA, P. The insecticidal efficiency of DDT deposits applied to apple foliage as solutions or emulsions 112

SELF-FERTILITY :
Induction of, in tree fruits. (Lewis and Crowe) 220

SHEPHERD, K. Seed fertility of the Gros Michel banana in Jamaica 1

SIMMONDS, N. W. Varietal identification in the Cavendish group of bananas .. 81

SLATER, C. H. W. (Rogers, Modlibowska, Ruxton and Slater) 126

SOIL STERILIZATION :
Steam pressure in, in bins. (Bunt) 89

SPRINKLING :
As an anti-frost measure. (Rogers, Modlibowska, Ruxton and Slater) .. 126

PAGE

STRAWBERRY :
Flower-bud initiation and development in early- and late-formed runners. (Robertson and Wood) 104
Stolon production by first-year plants in 1952. (Robertson and Wood) 231
Trials of burning and mowing plants after cropping. (Wilson and Rogers) 21
Var. Climax. Effect of long-term manurial treatments on the growth, yield and leaf nutrient status. (Bould and Catlow) 203

THOMAS, L. A. Stock and scion investigations. X. Influence of an intermediate stem-piece upon the scion in apple trees 150

THOMAS, W. D. E. (Bould, Thomas and Tolhurst) 301

THOMPSON, ELEANOR C., ROACH, W. A. and PRESTON, A. P. The reinvigoration of apple trees by inarching 175

TOLHURST, J. A. H. (Bould, Thomas and Tolhurst) 301

TOMATO :
Damping-off by species of *Pythium* and its control by use of formalin dust. (Montgomery) 245
Effects of different water-regimes on growth of plants under glass. (Salter) 258

TULIP :
Effects of deficiencies and excesses of some mineral nutrients on the growth of. (Hewitt and Miles) 237

VIRUS DISEASES :
Cherry. (Posnette) 44

WATER-REGIMES :
Effects of different, on the growth of plants under glass. Experiments with tomatoes. (Salter) 258

WILSON, DOROTHY J. and ROGERS, W. S. Trials of burning and mowing strawberry plants after cropping 21

WOOD, C. A. (Robertson and Wood) 104, 231

NOTICE TO CONTRIBUTORS

1. The **Journal of Horticultural Science** is an official organ of the Horticultural and Agricultural Research Station, Long Ashton, Bristol, and the Horticultural Research Station, East Malling, Kent.

The Publication Committee welcome horticultural papers from all other sources.

2. All **manuscripts** should be in double-spaced typewriting, with a good margin, and should be addressed to the Editors, East Malling Research Station, near Maidstone, Kent, England. Papers must be written concisely. Historical reviews should be as short as possible and only such references to literature as bear directly on the subject should be included. Tables and illustrations, if any, must be only such as are absolutely essential for clear presentation.

3. Authors of papers containing extensive **numerical observations** should consult the recommendations of the British Association Committee on Biological Measurements, 1927, obtainable from Burlington House, London, W.1. Price 6d. Arrangements have been made whereby original data too extensive for complete publication may be deposited at the British Museum (Natural History), London, S.W.7, or with the Royal Society of Edinburgh, 22 George Street, and thus be available for consultation by other workers. Full bibliographical reference to the publication in which the results are summarized must be supplied with the data.

4. Each paper must conclude with a concise and critically correct **summary** of its actual content. It should contain any new or verified constants as well as any other critical data of permanent value but not tables or graphs. Any organism mentioned should be given its scientific name.

5. Where a paper is of a highly technical nature it should be preceded by a brief **synopsis**, in which its contents are simply and clearly stated for the benefit of non-technical readers.

6. **References to literature** may be by numbers (in brackets) in the text corresponding to a numbered list at the end of the paper or by the Harvard system (author's name and date of publication). By either method, the papers cited should be listed alphabetically according to authors' names, followed by the date of publication. The title of the paper should next be given in full, followed by contracted, but strictly intelligible, title of source of publication, the volume and page numbers. Authors are responsible for the accuracy of their lists of references and should check them carefully in both typescript and proof.

7. The **scientific names** given in the "List of Common British Plant Diseases", published by the British Mycological Society (Cambridge University Press, 1944) and "Common Names of British Insect and other Pests", published by the Association of Applied Biologists (The Mendip Press Ltd., Bath, 1947) must be employed.

8. Authors in this country will be supplied with slip **proofs** of their papers; these they should correct with care immediately on receipt and return without delay, together with the original manuscript. Page proofs are not usually supplied to authors. Typographical errors, if any, should be corrected; small verbal alterations are permissible but substantial changes may not be made. Overseas authors should be willing to accede to editorial treatment of their contributions, if necessary, limited to methods of presentation, and leave proof correction to the Editors.

9. A single author will receive twenty-five **reprints** of his article free of charge. Special arrangements as to number of free reprints apply to papers by more than one author.

Additional reprints can be purchased at fixed prices, if ordered at the time of returning the corrected slip proofs and original manuscript.

10. The **copyright** of all articles and illustrations published becomes the property of the *Journal*, but Abstracting Journals may reprint the summaries, or translations of them, if desired. For permission to reprint more than this, application should be made to the Editors.

The publication of a paper in the *Journal* does not imply responsibility for, or agreement with, any statements or views expressed therein, but merely that the paper has been deemed to be of sufficient scientific interest to merit inclusion.

CONTENTS

PAGE

The Effects of Deficiences and Excesses of some Mineral Nutrients on the Growth of Tulip and Daffodil Bulbs in Sand Culture. By E. J. HEWITT and PEGGY MILES 237

Damping-off of Tomato by Species of *Pythium* and its Control by use of Formalin Dust. By NANCY MONTGOMERY 245

The Effects of Different Water-regimes on the Growth of Plants under Glass. I. Experiments with Tomatoes (*Lycopersicum esculentum* Mill.). By P. J. SALTER 258

Effects of Fruit Thinning by the Leaf Count Method on Yield, Size and Biennial Bearing of the Apple Duchess Favourite. By A. P. PRESTON 269

Molybdenum as a Plant Nutrient. III. The Interrelationships of Molybdenum and Nitrate Supply in the Growth and Molybdenum Content of Cauliflower Plants Grown in Sand Culture. By S. C. AGARWALA and E. J. HEWITT 278

Molybdenum as a Plant Nutrient. IV. The Interrelationships of Molybdenum and Nitrate Supply in Chlorophyll and Ascorbic Acid Fractions in Cauliflower Plants Grown in Sand Culture. By S. C. AGARWALA and E. J. HEWITT 291

Cover Crops in Relation to Soil Fertility and Fruit Tree Nutrition: The Effect of Grass on the Uptake of Total and Fertilizer Phosphate by Malling I Rootstocks. By C. BOULD, W. D. E. THOMAS and J. A. H. TOLHURST 301

Book Reviews 310

HORTICULTURAL ABSTRACTS

A Quarterly Journal for the research worker and progressive grower, issued regularly since 1931 by the COMMONWEALTH BUREAU OF HORTICULTURE AND PLANTATION CROPS at East Malling Research Station.

CONTENTS. A digest of world research on the problems of the fruit-, vegetable- and flower-grower, of the tobacco-producer and of the tropical and sub-tropical planter.

SUBSCRIPTION RATES. Subscriptions, which should be sent to *C.A.B., Central Sales Branch, Farnham House, Farnham Royal, Slough, Bucks:* Foreign, 50s. a volume or $7.00; British Commonwealth of Nations, 40s. a volume. Single copies 15s. or $2.10.

PRINTED BY HEADLEY BROTHERS LTD 109 KINGSWAY LONDON WC2 AND ASHFORD KENT